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Geology Series

Neogene crabs from Brunei, Sabah and Sarawak;
New pseudosciurids from the English Late Eocene;
Upper Palaeozoic Anomalodesmatan Bivalvia

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Neogene crabs from Brunei, Sabah and Sarawak

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Synopsis. Thirty-six species of fossil crab are described and figured from the Neogene of Sabah, Sarawak and Brunei. The following 3 genera, 31 species and 3 subspecies are new: *Dorippe frascone tuberculata, Calappa sexaspinosa, Podophthalmus fusiformis, Charybdis feriata bruneiensis, Portunus obvallatus, P. woodwardi, Galene stipata, Parthenope (Rhinolambrus) sublitoralis, Ampliura* (gen. nov.) *simplex, Drachiella guinotae, Iphiculus granulatus, I. miriensis, I. sexspinosus, Leucosia longiangulata, L. serenei, L. tutongensis, Myra brevisulcata, M. subcarinata, M. trispinosa, Nucia borneoensis, N. calculoides, N. coxi, Nucilobus* (gen. nov.) *symmetricus, Pariphiculus gselli beetsi, P. papillosus, P. verrucosus, Philyra granulosa, Typilobus marginatus, Palaeograpsus bittneri, Pinnixa aequipunctata, P. omega, Prepaeduma* (gen. nov.) *decapoda, Xenophthalmus subitus, Macrophthalmus (Mareotis) wilfordi.*

INTRODUCTION

Most of the material forming the basis of the present descriptions was collected by the Geological Survey Departments of Brunei, Sarawak and Sabah (formerly British Territories in Borneo) during the 1950s, and sent to the British Museum (Natural History) in 1958 and 1963–64. A small quantity of material was subsequently supplied by the Brunei Shell Petroleum Company Ltd. The material is only of broad stratigraphical value because of its uniqueness in the fossil record. Reliance was placed on the published ages for the beds by foraminiferal and molluscan workers (Nuttall 1961, Haile & Wong 1965).

A general description of the geology of Sarawak, Brunei and the western part of North Borneo was published by Liechti (1960). Locality S.4918 (see p. 4), originally surveyed by the Geological Survey as Miri Formation (Pliocene) age, was later re-assessed as being of ?late middle Pleistocene age (Wilford 1961). It is probable that locality S.5545 (=S.4965) is of similar age, containing as it does *Charybdis*, an in-shore genus with a modern aspect. The Pleistocene horizons were deposited in valleys which were cut into older strata and later flooded. The Pleistocene horizons represent shallower water than the Mio-Pliocene. Barnes (1968: 337) comments: '*Macrophthalmus* is today littoral, essentially sub-tropical and tropical frequently brackish or estuarine'; there is no reason to suppose that the fossils from Brunei came from a different sort of environment.

A few leucosiids were earlier collected by members of the Geological Survey of North Borneo from isolated areas in the north-east of Borneo; they are clearly from the older Miocene deposits but their stratigraphical control is poor.

The geological ages for these specimens are given in Collenette (1954) and Haile & Wong (1965).

All the material described in this paper is deposited in the British Museum (Natural History), Department of Palaeontology: register number prefix In.

THE FAUNA AND ITS PALAEOECOLOGY

The successive Mio-Pliocene crab faunas from north-west Borneo are unusual, in that they contain an abnormally high proportion of leucosiids (species and specimens) compared with the average of the Indo-West Pacific faunas. Table 1 compares the fossil faunas with data for the Indo-West Pacific region as a whole (taken from Serène 1968: 2804 species in 462 genera) at the present day, and for the nearest comparable Recent fauna, that of the Gulf of Thailand (Rathbun 1910: 207 species in 104 genera). The Gulf of Thailand was chosen because it most closely compares with the quiet waters of Borneo and also has a higher proportion of leucosiids than the normal shelf. The Gulf of Thailand fauna was largely taken by dredge from between the coast and the off-shore fringing islands, an area protected from the high energies of the open shelf with depths ranging from shoreline to about 50 m. The bottom is largely composed of sand and broken shell. Leucosiids generally live in such areas in relatively shallow water. They are weak, sluggish back-burrowers, lurking half-buried for passing prey. It is therefore suggested that the Mio-Pliocene horizons of Borneo were deposited in similar shallow (5–50 m), low-energy areas. The lithology of the rock confirms that the bottom was of sand and broken shell, particularly suited to the back-burrowing leucosiids.

Table 1 Distribution, by percentages in family of superfamily, of crabs from the Recent of the Indo-West Pacific (n = 2804 species in 462 genera; Serène 1968), the Neogene of Borneo (n = 36 species in 22 genera; herein) and the Recent of the Gulf of Thailand (n = 204 species in 107 genera; Rathbun 1910).

	Indo-West Pacific	Borneo (Neogene)	Thailand
Dromiacea	3.4	–	3.0
Raninoidea	0.7	3.0	–
Dorippoidea	1.6	3.0	1.0
Calappidae	1.3	3.0	3.0
Leucosiidae	10.0	65.0	16.0
Majoidea	27.7	3.0	16.0
Portunoidea	7.8	9.0	10.0
Xanthoidea	22.5	3.0	22.0
Hexapodidae	4.7	3.0	13.0
Pinnotheridae	4.3	9.0	5.0
Ocypodoidea	7.3	–	6.0
Grapsoidea	11.7	3.0	10.0

In addition, there are present in Borneo more commensal species of crabs than would be expected, since many are soft-shelled and consequently easily damaged or destroyed before burial. Although there is no direct fossil evidence, annelids and holothurians probably also thrived, which would account for the presence of a higher than average proportion of species (and specimens) of crabs commensal with these animals. The tube-like enrollment of the fossil commensal crabs suggests that sideways walking was already well established.

These suggested conditions invite comparison with the crab fauna collected from the Gulf of Siam (Thailand) by the Danish Expedition to Siam (1899–1900) and described by Rathbun, 1910. She (1910: 303) notes the position of the Gulf of Siam midway between the Indian Ocean and the West Pacific Ocean, and goes on to comment on the high number of new genera and species. This suggested an area particularly suited to speciation, a comment which might be equally true for the crabs of the Pliocene of Borneo. She further noted the abundance of small forms, especially Goneplacidae (*s.l.*) and Leucosiidae, which also show the same dominance in Borneo. Initially Rathbun attributed this bias to 'the zeal of the collector' but later came to realise that it was because the collection was taken from a sheltered arm of the sea. Rathbun recorded 204 species (of which 55 are inshore/estuarine species) in her report, compared with the 36 fossil species (2 inshore/estuarine) in the Borneo fauna here reported.

Some crab groups are clearly underrepresented in the Borneo fauna, particularly the Xanthoidea and Majoidea, but in the Gulf of Siam these are either associated with a very inshore position or found in close association with algae that appear to be absent in Borneo. Serène & Soh (1976), reporting on the Brachyura collected during the Thai-Danish Expedition (1966) from approximately the same area as Rathbun's material, commented particularly on the small size of the specimens. The great majority did not exceed 10 mm. This is also true of many of the species from Borneo, so it is not considered that the Borneo faunas contain a preponderance of juvenile forms.

The two genera *Macrophthalmus* and *Charybdis* from the Pleistocene of Borneo are found in many sublittoral, estuarine or brackish waters around the Indo-Pacific, the predatory *Charybdis* being the more fully marine.

The environment during the Pliocene remained relatively steady. One species (out of 29) survived from the Lower Miri to the Seria and 10 species survived from the Lower Miri to the Upper Miri; one species that appeared in the Upper Miri survived into the Seria Formation. No crabs have been collected from the topmost series of the Borneo Pliocene, the Liang Formation.

STRATIGRAPHY

According to Van Bemmelen (1970), the geosyncline formed on the base-levelled Cretaceous was sinking by the end of the Lower Tertiary, with subsidence continuing into the Upper Tertiary. The basin was being filled by clastic sediments from the central Borneo mountainous spine to the south and from surrounding land masses to the north (Sunda Continent). Umbgrove (1933) called this late cycle geosyncline, in which it lies between stable and mobile areas resulting in weak folding, an ideogeosyncline. Haile (1969) described the formations that make up what he called the North-west Borneo Geosyncline, going on to describe its organization and evolutionary history. He compared and contrasted it with Aubouin's (1965) geosynclinal couple model. Bol & van Hoorn (1980) believed that the parallel ridges were the result of mild compressional movements related to basement wrench faulting. These weak positive areas paralleling the present north-western coastline of Borneo probably acted as barriers to strong wave action, thus having the same effect as the fringing islands along the Gulf of Thailand today.

The Miri and Seria Formations of the Belait Group underlie about 647 km^2 of Quaternary in Sarawak and Brunei. Outcrops are mostly to be found in sea cliffs and road cuttings. The Belait Group consists of alternations of clays, sandy clays and sandstones. The main feature-forming beds are the thick sandstone sequences, from which much of the fossil crab fauna has come. The Miri Formation is 1954 m thick at Miri and it can be lithologically and (based on smaller benthonic foraminifera) palaeontologically divided into an upper (1323 m) and a lower (631 m) sequence. The Upper Miri is the more arenaceous, with more rapid but less regular alternations. The Seria Formation (up to 2000 m thick) is conformable with the underlying Miri Formation and is structurally and lithologically similar. It can be separated palaeontologically by the appearance of the foraminifer *Triloculina* 18 (Wilford 1961: 73). The lower beds of the Seria Formation are arenaceous, giving way to sandy and silty clays in the higher beds. The Seria Formation was deposited in a very shallow seaway, with even inshore lagoonal conditions; it was certainly shallower than the preceding Miri Formation sea.

Nearly 4000 m of sediment was deposited during the late Miocene and Pliocene filling of the geosyncline. An unsubstantiated estimate by Schuppli (1946: 4) suggests that during the Neogene of north-west Borneo 50,000 ft (*c.* 15,000 m) of sediment was deposited.

The Liang Formation, which is up to 3000 ft (*c.* 920 m) thick, overlies the Seria Formation, and was deposited on an erosional surface. The Liang is predominantly a marine transgressive series of poorly consolidated sands and clays, changing upwards into similar, but lagoonal or deltaic, sediments. No fossil crabs have been collected from the Liang Formation.

The top boundary of the Liang is an unconformable erosional surface with the overlying Pleistocene terraces. The cause of this was structural, following uplift *en bloc* of the coastal region of north-west Borneo. The denudation was followed by the Jerudong Cycle, which produced a system of mature valleys in which are deposited the Jerudong Terrace sands of ?late Middle Pleistocene age, estuarine or fluviatile in character. This deposit is never more than 10 m in thickness.

LOCALITIES

J.771. Mile 3½ on Labuk Road from Sandakan, Sabah. Undifferentiated Miocene Te$_5$–f (?Lower Miocene) (Fitch 1958).

NB.130, NB.132. South-east part of Silimpopon region near Tawau, Sabah. Silimpopon horizon of Wenk (1938) which is a clay band lying between the Simengaris Formation and Kapilit Formation, ?Lower Miocene (Te$_5$–f).

NB.11541. Headwaters of Silabukan River, *c.* 14 km east of Silabukan, Sabah. Segama Group, Tungku Formation, Middle Miocene (upper Tf).

S.4807. Calcareous nodules in sea cliffs at Penanjong, 5 km north-east of Tutong, Brunei. Pliocene, Seria Formation.

S.4918. Base of marine alluvium in road cutting, Mile 3¼ on Muara Road, 8 km north of Brunei Town, Brunei (?late middle Pleistocene – Wilford 1961: 102).

S.4965. See S.5545.

S.5536. Clay ironstone nodules in road cutting Mile 24½ on Tutong Road from Brunei Town, Brunei. Pliocene, Seria Formation.

S.5537. Clay ironstone nodules in road cutting Mile 21¼ on Tutong Road from Brunei Town, Brunei. Pliocene, Seria Formation.

S.5538. Mile 19½ on Tutong Road to Brunei Town, Brunei. Pliocene, Upper Miri Formation.

S.5539. Mile 17¾ on Tutong Road to Brunei Town, Brunei. Pliocene, Upper Miri Formation.

S.5544. Mile 13½ on Tutong Road to Brunei Town, Brunei. Pliocene, Lower Miri Formation.

S.5545 (= S.4965). Near Mile 13 on Tutong Road to Brunei Town, Brunei. Late Middle Pleistocene?

S.5548. Mile 12½ on Tutong Road to Brunei Town, Brunei. Pliocene, Lower Miri Formation.

S.5549. Mile 12¼ on Tutong Road to Brunei Town, Brunei. Pliocene, Lower Miri Formation.

S.5550. Mile 12 on Tutong Road to Brunei Town, Brunei. Pliocene, Lower Miri Formation.

S.10474. Sea cliff *c.* 1.5 km north-east of the mouth of River Trusan, south-west of Miri, Tanjong Batu area, Sarawak. Pliocene, Lower Miri Formation.

S.10475. In sea cliffs. 0.8 km north-east of the mouth of the Batang River, south-west of Miri, Sarawak. Pliocene, Lower Miri Formation but higher in succession than locality S.10474.

SYSTEMATIC PALAEONTOLOGY

Section **PODOTREMATA** Guinot, 1977

Subsection **ARCHAEOBRACHYURA** Guinot, 1977

Superfamily **RANINOIDEA** de Haan, 1841

Family **RANINIDAE** de Haan, 1841

Genus ***RANINOIDES*** H. Milne Edwards, 1837

TYPE SPECIES. By monotypy *Ranina laevis* Latreille, 1825, from the Recent (type locality unknown).

RANGE. Eocene to Recent.

Raninoides sp. Fig. 39

MATERIAL. Two fragmentary external moulds from locality S.5539. Upper Miri Formation: In 61915 (Fig. 39), In 61916.

DESCRIPTION. The full length of neither carapace is preserved, but it probably equalled twice the maximum width which occurs at about midlength; it is moderately rounded to weakly subcarinate in transverse section and longitudinally nearly flat. Gently convex posterolateral margins converge to a posterior margin somewhat narrower than the orbitofrontal margin, which occupies about three-quarters of the width. The very short anterolateral margins terminate at the basal scars of apparently rather small, obliquely-directed spines probably weaker than the flattened outer orbital spine. Posterior to the lateral spine the lateral edges are sharply downturned and the sides are inclined almost at right angles.

There is a very small tubercle set immediately behind the lateral spine a little closer to the midline than the margin; it is seen to advantage viewed posteriorly with the carapace held at eye-level. Similarly, a pair of longitudinal nodes are seen close to the midline a little in advance of and between the anterior extremities of short, deep gastrocardiac grooves extending over the median fifth of the carapace length. The cardiac region is weakly defined between the grooves and has a transverse pair of minute tubercles at the widest part.

DISCUSSION. The greater width in proportion to the length of *Raninella toehoepae* Van Straelen 1923, from the Miocene of Borneo, distinguishes that species from *R.* sp.

Section **HETEROTREMATA** Guinot, 1977

Superfamily **DORIPPOIDEA** de Haan, 1833

Family **DORIPPIDAE** de Haan, 1833

Genus ***DORIPPE*** Weber, 1795

TYPE SPECIES. By subsequent designation of Latreille 1810: *Cancer quadridens* Fabricius, 1793 (= *Cancer frascone* Herbst, 1785) [ICZN Opinion 688]; from the Recent of the Indian Ocean.

RANGE. Miocene to Recent.

Dorippe* (*Dorippe*) *frascone (Herbst) ***tuberculata*** subsp. nov. Fig. 1

DIAGNOSIS. Metabranchial regions more nodular than on nominal subspecies. An extra tubercle on either side of midline on the mesogastric region. Anterior part of cardiac region wider (*trans.*), and less prominent node at base of urogastric region. Sternal plates ridged with tubercles and with reduced spines on hepatic regions.

NAME. 'Tuberculate'.

HOLOTYPE. In 61853 (Figs 1a, b) from the Pliocene, Lower Miri Formation, locality S.5548. Paratypes In 61854–5 from S.5549 and In 61856 from S.5550, Lower Miri Formation.

DESCRIPTION. The carapace is subtrapezoidal in outline, almost flat longitudinally and only slightly arched transversely. The short, slightly convex anterolateral margins are barely interrupted where the cervical furrow reaches the margin; the anterior part of the posterolateral margins is nearly straight, deflected strongly outwards and, in the adult, ending in a sharp spine, but in specimens of approximately one-third the size it continues uninterrupted into the broadly rounded posterior part. A broad ridge bounds the deeply sinuous posterior margin. The orbitofrontal margin is not well preserved; it occupies rather more than half the carapace width. Basal scars indicate strong, obliquely-directed outer orbital spines and somewhat weaker spines at the lower inner orbital angle.

The cervical furrow is wide, fairly deep, and broadly V-shaped to its junction with the hepatic furrows, where it curves back to the margin; the branchiocardiac furrow, issuing from the same notch, is straighter laterally and much more rounded across the midline. Small hepatic regions are depressed and bordered above and below by low ridges, although the anterior ridge is not developed in the younger forms. The protogastric lobes tend to coalesce medially, partially obscuring the anterior process of the small lozenge-shaped mesogastric lobe. There is a low node at the base of each protogastric lobe, a similar one on the mesogastric, one at the base of the epibranchial lobes and another occupies almost all the much reduced mesobranchial lobe. At the base of the crescentic urogastric lobe deep pits, marking the posterior gastric muscles, are bounded by low, oblique ridges. More obvious on the larger specimen is a low, isolated node at the base of the urogastric lobe; the cardiac region has a small median lobe and is more nearly flask-shaped, less rounded than on the smaller carapaces, and acutely V-shaped ridges are more prominently developed. On the metabranchial lobes a weak groove isolates an ovate area on either side of the cardiac region and there is an obscure node anterior to the widest part of the region.

The upper surface of the larger carapace is finely pitted anteriorly, with granules grouped about the nodes; scattered granules on the branchial region become coarser and form rows parallel to the branchial furrows.

The 1st/2nd abdominal sternites are fused with the narrowly triangular, ridged 3rd sternite. The 4th sternites are subtrapezoidal in outline with much attenuated proximal angles leading down between the 5th sternites; near the anterior border a fissure extends half the distance to the midline; a steep ridge rising from the lower lateral angle recurves medially and there is a deep ovate pit on either side of the midline bordering the margin of the 5th sternite. The 5th sternite, scapuloid in outline, is bounded by a low, rounded ridge, while a more distinct median ridge forms the 'spine' terminating in a spinose 'acromion process' overlapping the 4th sternite. The rather more triangular 6th sternite has a convex basal margin and, medially, a well-rounded ridge descends steeply to the lateral margin; its 'acromion process' is formed from a secondary ridge issuing at about 45° from the median one.

DISCUSSION. This subspecies is very close to the nominal subspecies, but differs by having the tubercles along the ridges of the sternal plates. *Dorippe frascone* is distributed widely in the Indo-Pacific from East Africa to Japan and Australia. The nominal subspecies is known to live on sandy-silty or broken shell bottoms at 10–20m depth. None of the fossil specimens shows any sign of an epifauna, which is common on the Recent nominal species.

Superfamily **CALAPPOIDEA** de Haan, 1833

Family **CALAPPIDAE** de Haan, 1833

Genus ***CALAPPA*** Weber, 1795

TYPE SPECIES. By subsequent designation of Latreille, 1810: *Cancer granulatus* Linnaeus, 1758 [ICZN Opinion 712]; from the Recent of the Mediterranean Sea.

RANGE. Middle? Eocene to Recent.

Calappa sexaspinosa sp. nov. Figs 2a–c

DIAGNOSIS. Carapace with six spines on the flared clypeiform posterolateral margins; the dorsal surface is tuberculate with seven of the tubercles arranged elliptically on the branchial regions.

NAME. 'Six-spined'.

HOLOTYPE. In 61857 (Figs 2a–c), a small specimen possibly a juvenile. Pliocene, Lower Miri Formation, locality S.5548. Paratypes In 61858–61 from same locality.

OTHER MATERIAL. In 61862 (S.5544), an abraded specimen only possibly assigned to this species.

DESCRIPTION. The carapace is subtrapezoidal with the beaded edge of the anterolateral margin giving way to five broadly triangular spines, increasing in size posteriorly, followed shortly by a smaller spine on the flared posterolateral margin. This flared portion is very thin and is preserved only on the left side of the type. The posterior margin is probably as wide as the front, which occupies about half the carapace width immediately in front of the flare. The broadly triangular front is downturned and constricted just above the apex; it is produced slightly beyond the outer orbital angle. The orbits are subcircular and obliquely inclined; the upper orbital margins are thickened and have two feeble notches.

Broad furrows separate the median gastric and cardiac regions from the branchial regions. On each of the protogastric lobes, which are separated from the front by a shallow transverse depression, are two tubercles, the smaller, median one slightly in advance; anterior to the tubercles is a transverse row of eight granules. There is a large tubercle with a smaller one behind it on the mesogastric lobe; one on the urogastric and two in line on the cardiac region. Of the four tubercles on each hepatic lobe, the larger anterior pair are *en échelon* with the posterior pair. The epibranchial lobe has three tubercles in a transverse line, and the mesobranchial two small ones. On the metabranchial lobes, seven tubercles are arranged more or less elliptically. Two or three granules may be scattered within the enclosed area.

Fine, pitted grooves on the metabranchial lobes extend more or less parallel with the lateral margins.

The sides are directed sharply inwards and the pleural suture and concave buccal margins are bounded by ridges.

DISCUSSION. *Calappa sexaspinosa* is closest to the Recent species *C. lophos* (Herbst, 1782) but *C. sexaspinosa* has a very different distribution of tubercles. It differs from *C. hepatica* (Linnaeus, 1758) by its greater clypeiform extension of the posterolateral margin. *C. pustulosa* Alcock, 1896 is also very similar, but this species has virtually no clypeiform extension, giving a length/breadth ratio of 1:1 as opposed to 0.7:1 for *C. sexaspinosa*.

Superfamily **PORTUNOIDEA** Rafinesque, 1815

Family **PORTUNIDAE** Rafinesque, 1815

Subfamily **PODOPHTHALMINAE** Miers, 1886

Genus ***PODOPHTHALMUS*** Lamarck, 1801

TYPE SPECIES. By monotypy *Podophtalmus* [sic] *spinosus* Lamarck, 1801 [= *Portunus vigil* Fabricius, 1798]; from the Recent of the Indo-Pacific Region.

RANGE. Oligocene to Recent.

Podophthalmus fusiformis sp. nov. Figs 48–53

DIAGNOSIS. Carapace fusiform with straight, transverse upper orbital margins and well-rounded outer orbital angles; the lateral angle is at one third of the distance from the front.

NAME. 'Spindle-shaped'.

HOLOTYPE. In 62066 (Figs 48a, b). Paratypes In 62067 (Fig. 49), In 62068 (Fig. 50), In 62069 (Fig. 53), In 62070 (Fig. 51), In 62071 (Fig. 52), In 62072–96. All water-rolled internal moulds from locality S.5550, Lower Miri Formation.

DESCRIPTION. The carapace is fusiform in outline and about twice as long as broad. The rostrum (as seen on the latex mould) is very narrow, taking up only about a tenth of the orbitofrontal margin; it is steeply downturned and has a shallow median sulcus. Rather deep ocular constrictions lead to gently sinuous, almost straight upper orbital margins. The outer orbital spine was probably very weak and the lower orbital margin extends beyond the upper to the extent of the rostrum. The anterolateral margins, well rounded in front and gently concave behind, lead to strong, probably blunt spines set a little anterior to midlength, and directed slightly backwards. Sinuous posterolateral margins, rather longer than the anterolateral margins, lead by shallow coxigeal incisions to narrowly rounded posterior angles. The posterior margin is slightly convex and about half the width of the front. The cervical furrow curves forwards from immediately in front of the lateral spine, deepening at its junction with the hepatic furrow; it turns steeply backwards and inwards to the outer angle of the mesogastric lobe where it becomes deeper and more steeply inclined; at the base of the lobe it turns almost at right angles and terminates at a narrow incursion of the confluent urocardiac lobe.

The regions are distinct and slightly tumid. The mesogastric lobe is small and pentagonal; its very narrow, parallel-sided anterior process extends to the upper orbital margin and continues as an inconspicuous ridge onto the body of the lobe. A ridge on the lateral spine becomes obsolete as it progresses across the epibranchial lobe and the small, ovate mesobranchial lobes are rather more distinctly separated from the epibranchial than the metabranchial lobes. A weak branchiocardiac furrow follows the downward curve of the epibranchial ridge, reaching the margin anterior to the coxigeal incision. The urogastric and cardiac lobes together are broadly pentagonal and wider than the mesogastric lobe.

Only the male abdomen is preserved; it forms an attenuated triangle extending just into the 4th abdominal sternites; the narrow telson is about one sixth the length of the 6th somite, which is as long as the fused 4th/5th somites. The 3rd sternites are lozenge-shaped, the 4th subrectangular and the 5th–7th are chordate.

DISCUSSION. As preserved *Podophthalmus fusiformis* seems to lack the outer orbital spine of the genus. *P. vigil* (Fabricius) has orbits sloping backwards strongly, causing much reduced anterolateral margins; the lateral spines appear to be shorter than in *P. fusiformis*.

Subfamily **PORTUNINAE** Rafinesque, 1815

Genus ***CHARYBDIS*** de Haan, 1833

TYPE SPECIES. By subsequent designation of Glaessner, 1929: *Cancer sexdentatus* Herbst, 1783 (= *C. feriatus* Linné, 1758) [ICZN Opinion 712]; from Recent of the Indian Ocean.

RANGE. Oligocene to Recent.

Charybdis (Charybdis) feriata (Linné) ***bruneiensis*** subsp. nov. Figs 41, 42

1961 *Charybdis* sp. Ball, *in* Wilford: 102, 152; pl. 39 (*pars*).

DIAGNOSIS. A faint transverse ridge on the cardiac region.

NAME. 'From Brunei.'

HOLOTYPE. A part-decorticated carapace of a male, In 59015 (Figs 41a–c), from locality S.4965. Paratype In 59012 (Fig. 42), from S.4918. Both ?late Middle Pleistocene.

DESCRIPTION. The carapace is broadly ovate, the length being about four fifths of the width measured at the base of the lateral spines. In longitudinal section there is a moderate frontal depression; when viewed from the front the lateral margins are somewhat attenuated and slightly upturned. The orbitofrontal margin is about two thirds of the carapace width; no details of the front, which takes up half this distance, are preserved. Broadly ovate orbits are inclined a little outwards from the midline, and of the two notches in the slightly upturned upper orbital margin the outer is close to the outer orbital spine. Basal scars along the anterolateral margins indicate there were probably six spines. They appear to have been ovate in section, with the third about half the size of the first and succeeding pairs and the sixth thorn-like. Weakly rounded posterolateral margins lead by wide, shallow, slightly raised depressions for the 5th coxae to a broad, rounded posterior margin.

The regions are well defined, the median ones flatly tumid. On each protogastric lobe there is a short transverse ridge, almost uniting at the midline; from this ridge a triangular portion of each protogastric lobe encloses the anterior part of the semicircular mesogastric lobe. A stronger ridge crossing the broadest part of that lobe is similarly interrupted at the midline and immediately in front a low ridge develops into the anterior process which continues to the base of the small, rounded frontal lobe. Posteriorly the mesogastric lobe is divided by a furrow and its outer margins are lined with four or five granules. The urogastric lobe is represented by a small granular ridge. The cardiac region is lingulate in outline; anteriorly it is medially divided and there is a vague ridge; it becomes somewhat scabrous posteriorly. From the lateral spine a thin ridge curves the length of the epibranchial lobe. A broad depression encloses the mesobranchial lobe; between this lobe and the cardiac region is a low, rounded node and together the tumid areas form a semicircle about the mesogastric lobe.

A row of even-sized granules extends behind the upper orbital margin, there are a few atop the mesobranchial lobe and others of several diameters are scattered randomly over the dorsal surface.

On the underside deep marginal notches, giving way to shallow furrows, separate the 3rd from the 4th sternites. Shallower notches separate the 4th from the otherwise fused 5th sternites, the posterior angles of which are extremely drawn out to embrace the margin of the chordate 6th sternites; the 7th/8th are of much the same size and subreniform, while the 9th is much smaller and triangular in outline.

The right cheliped is slightly larger than the left. The anterior border of the merus has three spines of which the proximal one is the smallest. A large blunt process occurs at the inner angle of the carpus which has three spinules on the outer margin. The propodus, with five smooth costae, has two strong ridges with a spine at the distal end of each. There is also a spine on the anterior face near the carpal articulation. The fingers are about the same length as the palm.

DISCUSSION. Our species must be assigned to *Charybdis* (s.str.) because it does not have granular patches behind the epibranchial spine (*Gonioneptunus*), nor the curved posterior border of *Goniohellenus*. There are six anteriolateral teeth on the Brunei specimens, of which five are large; this rules out *Gonioinfradens* which has four large and two small. The Brunei species has only a very faint cardiac ridge; it is therefore unlikely to belong to *Goniosupradens* which has a distinct cardiac ridge. Of the 29 Recent species of *Charybdis (Charybdis)*, 7 fall within the geographic range of *C. bruneiensis: C. affinis* Dana, 1852; *C. annulata* (Fabricius, 1798); *C. feriata* (Linnaeus, 1758); *C. japonica* (Milne Edwards, 1861), *C. lucifera* (Fabricius, 1798), *C. milesi* (de Haan, 1835) and *C. rosaea* (Jacquinot & Lucas, 1853). Of these species *C. japonica, C. annulata* and *C. lucifera* are proportionately broader than *C. bruneiensis*. The other species differ in the spinosity of the chelipeds, except for *C. feriata* which is like *C. bruneiensis* in having four spines on the merus and three on the anterior border of the propodus. Similarly *C. bruneiensis* has the characteristic notched first anterolateral spine as in *C. feriata*. They differ in that *C. bruneiensis* does not have transverse ridges on the anterior part of the mesogastric and protogastric regions, but has a faint transverse ridge on the cardiac.

Genus ***PORTUNUS*** Weber, 1795

TYPE SPECIES. By subsequent designation of Rathbun, 1926: *Cancer pelagicus* Linnaeus, 1758 [ICZN Opinion 394]; from Recent, type locality not known. The International Commission on Zoological Nomenclature in reaching its decision on the type species appears to have overlooked the selection by H. Milne Edwards (July 1840) of *Portunus puber* (Linnaeus, 1767).

RANGE. Miocene to Recent.

Portunus obvallatus sp. nov. Figs 43–45

DIAGNOSIS. Carapace transversely subovate; anterolateral margins with eight spines, with the largest spine at the lateral angle; regions poorly defined and metabranchial region depressed.

NAME. 'Fortified'.

HOLOTYPE. In 61947 (♂, Fig. 43). Paratypes In 61948 (♂, Fig. 44), In 61949 (Fig 45), In 61950–6. All from locality S.5539, Upper Miri Formation. Paratype In 61957 from S.5549, Lower Miri Formation.

DESCRIPTION. A *Portunus* about half as long as broad and broadest at about midlength; moderately convex in longitudinal section, rather more steeply downturned in front and transversely almost flat. The narrowly rounded anterolateral margins have seven more or less evenly-sized granular spines followed by much larger sharp, slightly upturned spines at the lateral angles projecting straight out. The front is not well preserved; it takes up half the orbitofrontal margin, which occupies rather less than half the overall width. As far as can be made out, the outer orbital spine was weak, probably not extending beyond the front; the lower orbital margin extends beyond the thinly ridged upper orbital margin. A weak anterior-facing 'ridge' reaches only a short distance along the lateral spine and the epi- and metabranchial lobes are slightly tumid rather than ridged. The cervical furrow is straight where it crosses the midline, then turns sharply forward and becomes obsolete before reaching the margin. There is a short longitudinal groove at the base of the poorly-defined mesogastric lobe and on either side of the groove are one or two granules; the anterior mesogastric process is barely separated from the protogastric lobes. The cardiac region is broadly hexagonal and wider than the mesogastric lobe. On either side of the cardiac region is a low, rounded 'ridge' with a tubercle at its posterior end, and the metabranchial lobe is depressed against this ridge and behind the epigastric lobe.

DISCUSSION. The diminutive marginal spines anterior to the prominent one at the lateral angle distinguish *P. obvallatus* from *Portunus woodwardi* sp. nov. (below); the posterior margins of the latter are angular rather than sinuous as in *P. obvallatus* which also has a less lobate dorsal surface. The arrangement of the lateral spines is not unlike that of *Portunus sanguinolentus* (Herbst, 1769); otherwise there is no obvious comparison with other species figured from Sagami Bay by Sakai (1965) or Hawaii by Edmondson (1954).

Portunus woodwardi sp. nov. Figs 46, 47

DIAGNOSIS. Carapace with eight anterolateral spines, the seventh vestigial and the eighth at the lateral angle; the mesogastric lobe is partially divided medially and its anterior process extends to the base of the frontal lobes.

NAME. After Dr H. Woodward, palaeontologist.

HOLOTYPE. In 61923 (♂, Figs 46a, b). Paratypes In 61924 (♂, Figs 47a, b), In 61925–36. All from Pliocene, Lower Miri Formation, of locality S.5548. Paratypes In 61937–45 from Upper Miri Formation, S.5539.

DESCRIPTION. The carapace is broader than long, with the anterolateral margins forming a broad semicircle with the front. The broadly ovate orbits take up the outer fourths of the orbitofrontal margin. The front is not well preserved on any of the available specimens. There is a single notch in the upper orbital margin and behind the short, triangular outer orbital spine are six more or less even-sized subquadrate spines followed by a smaller one which is more conspicuous on the internal mould and, for the most part, incorporated by the shell thickness into the much attenuated spine at the lateral angle. The interstices between the spines are deeply U-shaped and alternate pairs are marked by a short groove extending onto the carapace. Short posterolateral margins converge rapidly to moderate excavations for the 5th coxae and the posterior margin is weakly convex.

Low, oblique ridges separate subrectangular protogastric lobes from frontal and epigastric lobes. The hepatic region is separated by a slight furrow from the gastric region, and from the branchial region by a forwardly curved epibranchial ridge extending from the lateral spine to ovate mesobranchial lobes. The uro- and mesogastric lobes form a single, almost pentagonal area and the slender, slightly tapering anterior process reaches the base of the frontal lobes. The cardiac region is pentagonal and somewhat elongated posteriorly; anteriorly it is weakly divided medially by a furrow which extends a short way onto the urogastric lobe. The metabranchial region has two almost confluent nodes close to the epibranchial and cardiac borders, but is depressed laterally. There is a small ovate node tucked between the mesobranchial lobe and cardiac region.

The tumid areas of the dorsal surface are crowded with rather coarse granules which become sparser and smaller posteriorly.

On the underside of the male the 1st–3rd sternites are transversely narrowly triangular; the 4th are trapezoidal and somewhat indented by the abdominal trough; the 5th and 6th are subrectangular, tapering a little medially; the 7th are rather more rectangular, while the 8th are triangular in outline. Numerous granules crowding the surface become finer posteriorly.

One specimen, In 61924 (Figs 47a, b) has on its left side a swelling typically caused by a parasite, *Bopyrus* sp.; its remarkably large size so strongly affected the natural development of the branchiostegal areas, as well as the dorsal region, that all the anterolateral spines became completely atrophied and the lateral angle rounded. This parasite is of uncommon occurrence among fossil portunids.

DISCUSSION. While no precise details of the front of *P. woodwardi* sp. nov. are available for comparison, it is nonetheless close to *Portunus arabicus* (Woodward, 1905) from the ?Pliocene of the Mekran coast, but in the latter the anterior process of the mesogastric lobe terminates at the transverse 'ridge'; the mesogastric lobe of *P. woodwardi* is proportionately larger, less rounded than that of *P. arabicus* and is divided by a median furrow. *P. woodwardi* is also close to *Portunus gladiator* Fabricius, 1798, but in the latter species anterolateral spines are more triangular and the spaces between them V-shaped.

Superfamily **XANTHOIDEA** Dana, 1851

Family **XANTHIDAE** Dana, 1851

Genus ***GALENE*** de Haan, 1833

TYPE SPECIES. By monotypy *Cancer bispinosus* Herbst, 1783 [ICZN Opinion 85]; from Recent of the Indo-Pacific.

RANGE. Miocene to Recent.

Galene stipata sp. nov. Figs 54, 55

DIAGNOSIS. *Galene* with extraorbital spine and three lateral spines.

NAME. 'Guarded'.

HOLOTYPE. In 59014 (Figs 54a–d) from the Pliocene, Lower Miri Formation of locality S.4965. Paratypes: In 61958 (Fig. 55), In 61981 from S.5548, In 61971–80 from S.5549, both Lower Miri Formation; In 61961–70 from Pliocene, Upper Miri Formation, S.5538; In 61959–60 from Pliocene, Seria Formation, S.5537.

DESCRIPTION. The anterior mesogastric process is parallel-sided for half its length; thereafter it tapers to a point terminating level with the upper orbital margins. The front follows the carapace curvature and is half the width of the orbitofrontal margin; it has a narrow median notch extending back as a groove on the dorsal surface; the inner pair of lobes are rounded, very close together and extend beyond the outer pair which form the inner orbital spines. The orbits are subovate and the wide upper orbital margin, bounded in part by a fine groove, has a beaded row of granules interrupted by two feeble notches; between the granules and groove there is a row of pits.

Where it crosses the midline, the cervical furrow is acutely V-shaped and very shallow round the base of the mesogastric lobe; from the forward angle of the mesogastric it extends in a moderately deep, broad curve forwards and outwards to the margin. The median part of the furrow becomes obsolete as growth advances and on larger specimens a false impression of its course is given by the stronger, straighter groove between the urogastric and cardiac lobes. Within the cervical furrow the posterior gastric pits are set very close together and, on specimens ranging up to at least 12.0 mm in carapace width, cuneiform pits mark the position of the internal mandible adductor muscles.

Granules of several diameters crowd the dorsal surface, those posterior slightly the larger. Sub-surface shell layers show groups of pits particularly on the more tumid areas except the cardiac region where they are arranged marginally.

The 1st–3rd abdominal somites are fused in both the male and female, the distal margin is straight, medially concave, laterally convex; a depression, broadening posteriorly, deepens from the medial concavity. A notch between the 1st–3rd and 4th sternites leads back at *c.* 65° and gives way to a broadly curved groove. The 4th sternites are rhomboidal, a broad groove runs from the distal notch to a broadly rounded posterolateral angle. The 5th sternites are half the length of the 4th and subrectangular, the 6th are somewhat longer and more quadrate, the 7th are about half the width of the 6th while the 8th are much reduced and triangular. The abdominal trough extends almost to the anterior margin of the 4th sternites. There is a scattering of granules on the 1st–3rd sternites, particularly near the margins, and on the neighbouring parts of the 4th sternites. The male abdomen tapers moderately from the 3rd somites and the telson-apex is broadly rounded. The ovate female abdomen reaches its broadest at the 4th somite; the length of the rounded-triangular telson exceeds that of the 6th somite.

DISCUSSION. Young forms are somewhat flatter in longitudinal section, more distinctly lobate and granulated and at this stage closely resemble *Lobonotus* spp. – particularly in the small node flanking the cardiac region separated from the metabranchial lobe. In *Galene stipata* this node becomes disproportionately larger as growth advances and less sharply separated from the metabranchial lobe. Also, the protogastric lobes of *G. stipata* are entire, with no tendency towards the bilobed development common to *Lobonotus*.

The present species from Brunei is very close to *Galene obscura* Milne Edwards, 1865, in that it has the extraorbital spines, a groove on the metabranchial region and a spine at the posterolateral angle. Their length/width proportions are very similar but Milne Edwards (1865) recorded five spines on the lateral margin of *G. obscura* whilst only three can be determined on *G. stipata*. *Galene stipata* differs from *Galene bispinosa* (Herbst, 1783) in all the characters stated by Milne Edwards for that species.

Superfamily **PARTHENOPOIDEA** Macleay, 1838

Family **PARTHENOPIDAE** Macleay, 1838

Genus ***PARTHENOPE*** Weber, 1795

TYPE SPECIES. By subsequent designation of Rathbun, 1904: *Cancer longimanus* Linnaeus, 1758 [ICZN Opinion 696]; from Recent of the Indo-Pacific Ocean.

Subgenus ***RHINOLAMBRUS*** Milne-Edwards, 1878

TYPE SPECIES. By original designation *Cancer contrarius* Herbst, 1804 from Recent of the East Indies.

Parthenope (Rhinolambrus) sublitoralis sp. nov. Fig. 40

DIAGNOSIS. The carapace is pentagonal, nearly as long as broad, with its margins lined with tubercles increasing in size posteriorly; the branchial regions are ridged and the dorsal surface bilaterally ornamented with unequal-sized granules.

NAME. 'Below the shore'.

HOLOTYPE. In 61917 (Figs 40a, b) from locality S.5548, Lower Miri Formation. Paratypes In 61918–22 the same locality and horizon.

DESCRIPTION. The carapace is broadly pentagonal, almost as long as broad and deeply depressed between the gastric and branchial regions and, in side view, highest at the cardiac region. There are two or three small granules on the very short anterolateral margins. The short anterior part of the posterolateral margin curves broadly with the lateral angle, and the posterior part is nearly straight; the margins are lined with seven or eight granular tubercles gradually increasing in size posteriorly. A thin ridge bounds the gently convex posterior margin and there is a small tubercle at each angle. The orbitofrontal margin is narrow and slightly elevated. As preserved the rostrum appears to have been not much produced, moderately downturned and sulcate.

From an obscure marginal notch the cervical furrow curves broadly to the angle of the mesogastric lobe, turns sharply inwards and terminates in a pit on either side of the midline. The hepatic region is small and depressed with three or four granules. Shallow constrictions separate the protogastric lobe from the small, subovate mesogastric lobe, the anterior process of which continues to the base of the rostrum. On the protogastric lobes are two rows of four granules, the innermost pair the larger; the mesogastric lobe has two large granules each flanked by a small one, and small granules flank a median one on the urogastric lobe. Several granules encircle a larger median one on the cardiac region and the oblique branchial elevations are also ornamented with unequal granules.

Parallel granulated ridges on the subhepatic and pterygostomian regions extend to the lower outer angle of the orbit. A single ridge on the branchiostegite curves in to the lower angle of the buccal margin, which is quadrate, wider than long.

Of the thoracic sternites, the first pair are very small and slightly indented from the 2nd; these are weakly delineated from the 3rd, which are subovate and deeply separated medially; together they form an obtuse triangle bounded by a raised rim. The 4th sternites are quadrate and the 5th–8th rectangular; on each of the latter is a median granule and another occurs on the outer border.

DISCUSSION. The new species is very similar to *Rhinolambrus pelagicus* (Rüppell, 1830) from the Recent of the Red Sea, but has tubercles on the branchial regions in lines separated by deep branchial grooves. Each axial region has a single large tubercle with a varying number of subsidiary tubercles, compared with the more numerous but randomly distributed tubercles on *R. pelagicus*. A Recent species from an unknown locality, *Rhinolambrus contrarius* (Herbst, 1804) has a similar distribution of tubercles but differs by having only one groove crossing the branchial region instead of the two in *R. sublitoralis*. All other species of *Rhinolambrus* have branchial processes and are therefore clearly distinct from *R. sublitoralis*. There is some similarity between the new species and *Platylambrus serratus* (H. Milne Edwards, 1834) from the Recent of the 'Indian Ocean' [*recte* west Central America, see Rathbun, 1925: 516], but the latter has the hinder part of the posterolateral margins more concave and there are a greater number of tubercles on the anterior part of the posterolateral margins.

Superfamily **LEUCOSIOIDEA** Samouelle, 1819

Family **LEUCOSIIDAE** Samouelle, 1819

Genus ***AMPLIURA*** nov.

TYPE SPECIES. *Ampliura simplex* gen. et sp. nov. from Pliocene, Seria Formation of Borneo.

DIAGNOSIS. Wide subcircular female abdomen, buccal cavity initially widening forwards; non-spinate, beaded lateral margins. Length to width ratio 0.85 or less. Hepatic furrows vestigial or absent.

NAME. From Latin *amplus*, large + Greek οὐρά, tail. Feminine.

DISCUSSION. Differs from *Typilobus* by its globose female abdomen and beaded lateral margins. *Nucia* also has a globose female abdomen, but differs from *Ampliura* by its spinate lateral margin and normal leucosiid buccal cavity.

In the weak development of furrows, except for the furrows bounding the cardiac region, and absence of lateral spines *Typilobus obscurus* Quayle & Collins, 1981, from the Upper Eocene of southern England, may be an early member of the genus but its abdomen is unknown; it otherwise differs by being almost circular in outline. Another species with scarcely defined regional furrows and smooth lateral margins is *Typilobus modregoi* Via Boada, 1969, but maximum width appears to occur anterior to the middle, unlike most leucosiids which have their greatest width at the middle or just posterior to it. A second species from the same horizon and locality, *Typilobus boscoi* Via Boada, 1969, resembles *Ampliura* with its female abdomen (Gómez-Alba, 1988) and vestigial hepatic grooves, but differs from it in having spinate lateral and posterior margins and normal leucosiid triangular buccal cavity.

Ampliura simplex gen. et sp. nov. Fig. 3

DIAGNOSIS. The carapace is subovate, without lateral spines and only feebly indented at the cervical notch; the cervical and hepatic furrows are inconspicuous.

NAME. 'Simple', from the absence of any marginal processes.

HOLOTYPE. In 62157 (Fig. 3), a female from locality S.5537, Seria Formation.

DESCRIPTION. The carapace is transversely subovate with broadly rounded lateral angles, the length being about three-quarters of the breadth; transversely and longitudinally flattened and with hardly any postfrontal depression. Only the merest indentation at the cervical notch interrupts the broadly rounded anterolateral margins. The orbitofrontal margin occupies about half the carapace width; no details of the front are preserved, but the orbits are very small and circular.

The hepatic and lateral part of the cervical furrows are present as vague lines between the granules; the grooves separating the urogastric and cardiac lobes from one another and from the branchial regions, however, are more clearly defined. The mesogastric lobe is discernible rather by the grouping of granules than by any clear-cut groove. The cardiac is broader than the mesogastric lobe and more or less shield-shaped; it very slightly indents the urogastric in front and probably almost touches the posterior margin behind.

The entire dorsal surface is densely covered in flattened granules of several diameters extending over the rounded lateral edges and sides.

There is a fine groove above the subtriangular pterygostomian region; the outer shell surface near the front is missing: had it been preserved, this part of the region would in all probability have been visible in dorsal view. Oviducts open into fifth sternites.

DISCUSSION. See generic discussion.

Genus ***DRACHIELLA*** Guinot *in* Serène & Soh, 1976

TYPE SPECIES. By original designation *Lithadia sculpta* Haswell, 1880, from the Recent of Fitzroy I., Queensland, Australia.

Drachiella guinotae sp. nov. Fig. 9

DIAGNOSIS. Regional grooves divide the branchial region into its component epi-, meso- and meta- regions. Cardiac region circumscribed by furrows. Protogastric region clearly differentiated. Eyes visible on dorsal surface.

NAME. In honour of Dr Danièle Guinot.

HOLOTYPE. A female carapace, In 61863 (Figs 9a–c) from *c.* 1 mile NE of R. Trusan, SW Miri, Tanjong Batu area, Sarawak; Lower Miri Formation.

DESCRIPTION. Carapace transversely subovate, length almost 0.8 of the width, widest about midlength; steeply rounded transversely and in side view steeply rounded from behind the front to the cardiac region which forms a second prominence. Distinct furrows extend from the posterolateral angles to the front, at which point they are separated by the ridged anterior mesogastric process; lobulate marginal tubercles completely isolated from all the dorsal regions. There is a deep indentation between paired tubercles at the lateral angles and one on the anterolateral margins. The straight posterolateral margins have a tubercle behind the lateral pair and another just before the ridged intestinal lobe. The intestinal lobe overhangs and gives a false impression of the posterior margin from which it is separated by a fine groove. From the anterolateral tubercle a short concave tuberculate ridge leads to the outer angle of the orbit. A thin ridge of four to five granules forms the upper orbital margin barely divided from the narrow, almost straight, bluntly depressed front. A groove leading back from the front separates prominent frontal lobes joined behind by the anterior mesogastric process. The very small circular orbits are directed obliquely upwards and divided by a strong septum from somewhat larger, deeper antennal fossae. The epistome appears to have been narrow and acutely V-shaped.

The cervical furrow is obtuse and very shallow where it crosses the midline about mid-carapace length; becoming much broader, it turns abruptly forwards and outwards to the lateral margin; crossing the margin it divides a lineal subhepatic lobe and a stronger, tapering ridge on the pterygostomian region. A furrow separates obliquely inclined elliptical epigastric lobes from fairly large quadrate hepatic and triangular protogastric lobes; the latter barely separated from one another by an ill-defined furrow. A strong furrow separates the circular cardiac region from the intestinal lobe. Large epibranchial lobes are separated by a furrow (containing a row of tubercles extending from the smaller mesobranchial lobes to the cervical furrow) from a thin, rather sinuous metabranchial lobe.

Bilaterally arranged tubercles of several diameters crowd the dorsal surface; one, more conspicuous, is set behind each upper orbital margin. The more prominent of the cardiac tubercles form a saltire anteriorly with a row at its base, the whole surrounded by a ring of granules. Deep in the grooves many of the tubercles are entire – a few almost mammillate – but the vast majority are cratered with a single median granule.

The buccal margin tapers towards the front and its margin forms a line with the outer orbital margin. The pleural suture is bordered with a line of very small cratered granules while others similar to those on the dorsal surface tend to form rows on the branchiostegite. The abdominal trough is ovate and each sternite has a tubercle at its lateral edge.

DISCUSSION. The four species assigned by Guinot to the genus *Drachiella, D. sculpta, D. morum* Alcock, 1896, *D. lapillula* Alcock, 1896 and *D. aglypha* Laurie, 1906 have the branchial region entire. *D. guinotae* appears to show the primitive condition in which the subdivisions of the branchial region are defined by furrows. The protogastric, epigastric, hepatic, cardiac and intestinal regions are similarly defined by furrows. The furrow separating the hepatic from the protogastric regions is less strongly impressed than the others. The frontal region of *D. guinotae* is less wide (*trans.*) than it is in *D. morum*, and the eyes are more anteriorly situated, and therefore less visible, than in *D. morum*, but more so than in *D. lapillula*.

Genus ***IPHICULUS*** Adams & White, 1848

TYPE SPECIES. By monotypy *Iphiculus spongiosus* Adams & White, 1848 [ICZN Opinion 73], from Recent of the Phillipine Islands.

RANGE. Pliocene to Recent.

Iphiculus granulatus sp. nov. Figs 15, 16, 18

DIAGNOSIS. Carapace subovate with a granulated dorsal surface; no tubercles developed on the pterygostomian region.

NAME. 'Granulated'.

HOLOTYPE. In 61868 (♀, Figs 15a–c). Paratype In 61869 (Figs 16, 18). All from locality S.4807, Seria Formation.

DESCRIPTION. The outline of the carapace is closely similar to that of *Iphiculus miriensis* sp. nov. (below), but there is no overshadowing tubercle on the pterygostomian region, which is somewhat less tumid. The orbitofrontal margin is not well preserved; it occupies about two-fifths of the carapace width. The rostrum is sulcate and there are two notches in the thin, upturned upper orbital margin.

With the exception of a narrow depression behind the front and the bases of the median furrows the dorsal surface is densely crowded with granules of several diameters.

The pleural suture is lined with granules and the underside of both sexes is similar to that of *Iphiculus miriensis* sp. nov.

Iphiculus miriensis sp. nov. Figs 11–14

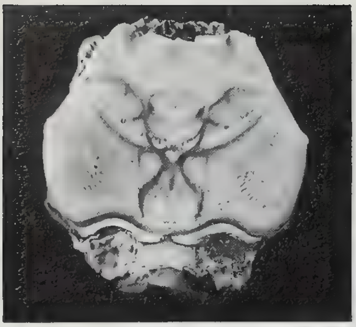
DIAGNOSIS. Carapace subovate with six blunt spines on the lateral margins; the dorsal surface is ornamented with 25 small, regularly arranged tubercles.

NAME. 'From Miri'.

HOLOTYPE. In 62123 (Fig. 11). Paratypes In 62124–6 (Figs 12–14), In 62127 (♂), In 62128–30 (♀), In 62132–8 (indet. sex). All from locality S.5548, Lower Miri Formation. Paratypes In 62139–43 from S.5549, In 62144 from S.5550, all from Lower Miri Formation. Paratypes In 62121–2 from S.5539, Upper Miri Formation.

DESCRIPTION. The carapace is subovate in outline, the length being about 0.8 of the width measured between the 2nd–3rd lateral spines; longitudinally it is domed with a shallow frontal depression, and flatly domed transversely. The well-rounded anterolateral margins are armed with four blunt spines increasing in size posteriorly; the anterior one is often obscure, almost granular, and overshadowed by a large spine immediately below on the pterygostomian process. The posterolateral margins are longer than the anterolateral margins; there are two granular spines, more noticeable on young specimens, and the space between them is twice the distance which separates the foremost from the spine at the lateral angle, and the hindmost from a short, sharp spine at the posterior angle. The posterior margin is about as wide as the front, slightly concave and narrowly rimmed. The very narrow, slightly upturned front occupies about one third of the carapace width; the rostrum is small, triangular and strongly deflected downwards; the margins are upturned by a continuation of the upper orbital margins, in which there are two notches. The narrowly ovate orbits are inclined about 45° to the midline and partially separated from rather large, subcircular antennal fossae.

The cervical furrow can just be traced on some specimens; it runs slightly back for a short distance from the margin before terminating in a shallow pit, where it joins an obscure, partially developed furrow curving from the outer orbital notch and delineating the hepatic region. A broad groove separates the confluent median gastric and cardiac regions from the large, tumid intestinal region. Broad, but shallow, furrows separate the cardiac and intestinal regions from the branchial regions. There are normally 25 small tubercles on the carapace in all. There are four on each protogastric lobe, the foremost pair forming an upturned curving row with one on each hepatic region, and the hinder pair, a downward curving row with one on each epibranchial lobe; a shorter row is composed of one tubercle on each meso- and metabranchial lobe, while another two, one behind the other, on the metabranchials lie opposite two transverse cardiac tubercles; the urogastric lobe has three tubercles in an inverted triangle. Each tubercle is ringed by, and covered with, small pustular granules, while numerous granules of several diameters are scattered over the elevated parts of the carapace and extend onto the lateral spines.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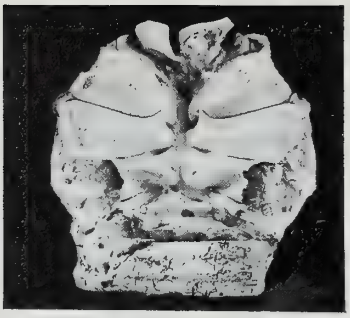
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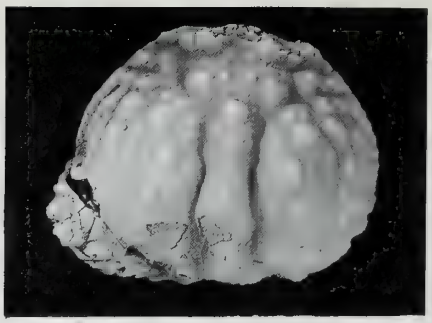
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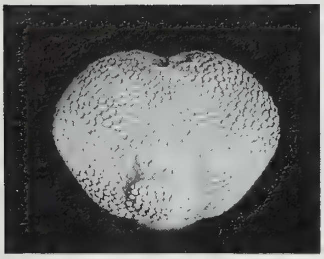
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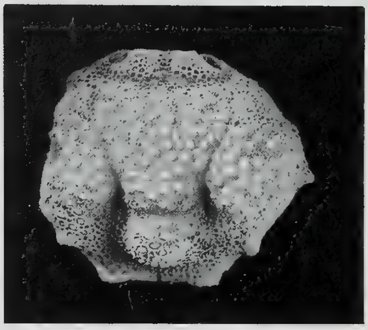
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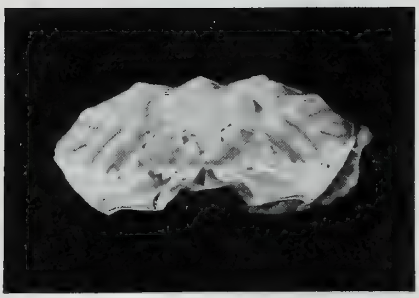
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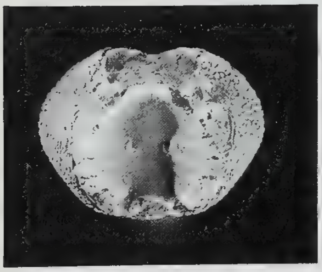
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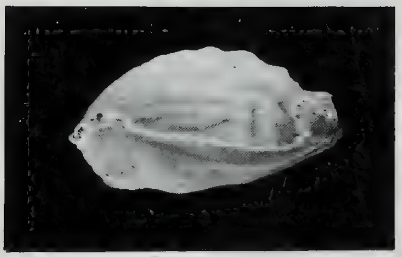
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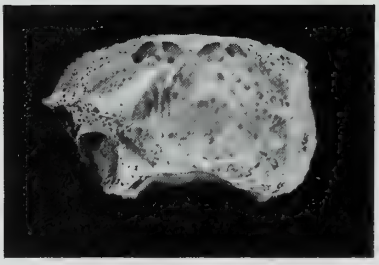
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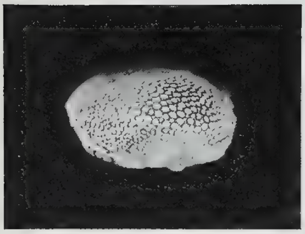
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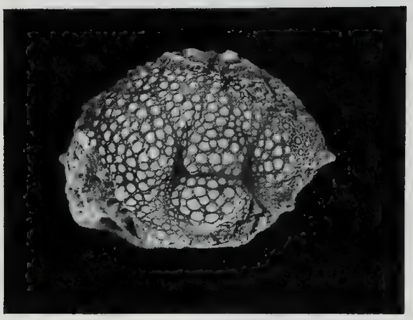
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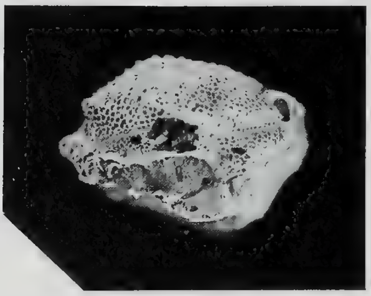
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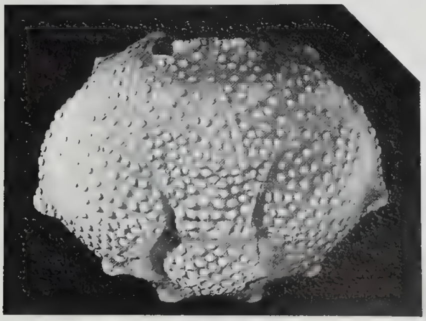
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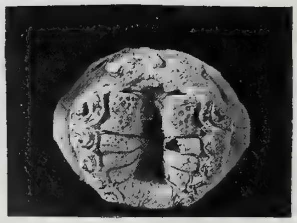
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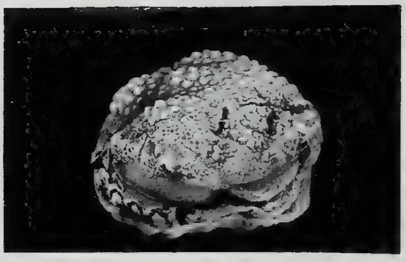
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A row of granules generally lines the pleural suture, and the pterygostomian region is well delimited and tumid. The branchiostegite becomes devoid of granules posteriorly. The buccal margins are straight and divergent.

Of the sternites, the 1st and 2nd are reduced to a narrow transverse ridge with a median granular prominence; the 3rd and 4th sternites are triangular and of similar size, while the 5th–8th are subrectangular and decrease in size posteriorly.

In the male the abdominal trough extends almost the full length of the 3rd sternites and the deep, steep-sided walls are ridged above by a line of coarse granules. This ridge is not developed in the female in which the abdominal trough is broadly concave and, except anteriorly, the sternites are less studded with granules.

Iphiculus sexspinosus sp. nov. Figs 17, 19

Diagnosis. Carapace subovate with six marginal spines and a prominent pterygostomian tubercle; the cardiac and intestinal tubercles are vestigial and the dorsal tubercles are restricted to two transverse rows anteriorly.

Name. 'Six-spined.'

Holotype. In 61864 (♂, Figs 17a, b) from locality S.5536, Seria Formation. Paratypes In 61865 (Fig. 19), In 61866 from S.5539, Upper Miri Formation; In 61867 from S.5537, Seria Formation.

Description. The outline of the carapace and its marginal spines is essentially similar to that of *Iphiculus miriensis* sp. nov. (p. 11). The front is slightly produced; the tip of the rostrum is obscured, but behind it is sharply divided medially by a deep V-shaped cleft which continues back a short way onto the carapace. The upper orbital margin is formed by three short equidistant spines, deeply divided by notches; the median spine is directed a little upwards.

The cardiac and intestinal tubercles are not seen on the outer shell surface, although they are vestigially present as structures on an inner-shell layer; the other dorsal tubercles are much reduced in size and tend to be restricted to two anteriorly distributed rows each comprising six tubercles.

Discussion. Of the present collection *I. sexspinosus* probably comes closest to the type species *I. spongiosus*, the latter having a rather coarser surface ornament and only a single line of vague 'tubercles' corresponding to the posterior row on *I. sexspinosus*. The long lateral spine typical of *I. spongiosus* reaches a length of about a fifth of the carapace width, whilst in *I. granulatus* it would probably have reached about a quarter of the carapace width. The granulation of *I. granulatus* sp. nov. (p. 11) is coarser than that of *I. sexspinosus*, and the secondary tubercular ornament is wanting; the cardiac region is less well defined. The greater number and larger size of secondary tubercles distinguishes *I. miriensis* from *I. sexspinosus*.

Genus ***LEUCOSIA*** Weber, 1795

Type species. By subsequent designation of Holthuis, 1959: *Cancer craniolaris* Linnaeus, 1758 [ICZN Opinion 712]; from Recent of the Indo-Pacific.

Range. Miocene to Recent.

Remarks. The International Commission on Zoological Nomenclature appears to have overlooked the selection by H. Milne Edwards (October, 1837: pl. 25, fig. 1) of *Leucosia urania* Fabricius, 1798 as type species.

Leucosia longiangulata sp. nov. Figs 25, 26

Diagnosis. The carapace is broadly rhomboidal with a narrow, slightly produced front and thin, elongate lateral angles; the deep thoracic sinus terminates in a pit from which a groove extends to the lateral margin.

Name. From Latin *longus*, long + *angulatus*, with angles.

Holotype. In 61890 (Figs 25, 26) from locality S.10474, Lower Miri Formation.

Description. The carapace is rhomboidal in outline, about one-seventh longer than wide and much narrowed anteriorly. The front is slightly produced, vaguely tridentate with the sharply downturned rostrum taking up the middle third; the triangular elevation above is rounded. There is very little constriction behind the front and the gently convex anterolateral margins lead to rather elongate lateral angles, commencing about one third distant from the front. The lateral edge is sharp and finely granulated, the granules continuing only a short distance beyond the lateral angles. The posterolateral margins are a little recurved before acute posterior angles. The posterior margin is somewhat extended, flattened, straight and bordered with granules; it is about twice the frontal width.

The thoracic sinus is deep and ends well in front of the 1st limbs in a rather deep, obtusely ovate pit which has a narrow groove passing upward round the lateral edge immediately before the lateral angle.

Discussion. See p. 15.

Leucosia serenei sp. nov. Figs 20–23

Diagnosis. The carapace is rhomboidal with the front moderately produced and narrow; the thoracic sinus is broad and terminates in an obscure depression.

Name. In honour of Dr Raoul Serène.

Holotype. In 61870 (Figs 20a–b). Paratypes In 61871 (Fig. 21), In 61872 (Fig. 22), In 61873 (Fig. 23), In 61874–80. All from locality S.5548, Lower Miri Formation. Paratypes In 61881–4 from S.5539, Upper Miri Formation.

Fig. 1 *Dorippe frascone tuberculata* subsp. nov. **Holotype** In 61853 from S.5548, Lower Miri Formation, × 1. a, dorsal view; b, ventral view.

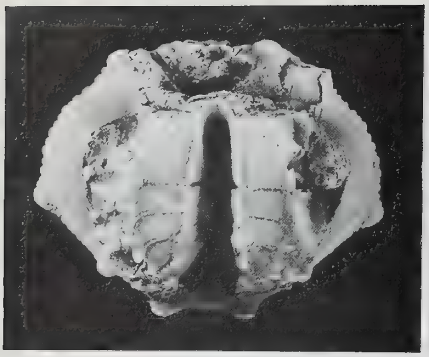
Fig. 2 *Calappa sexaspinosa* sp. nov. **Holotype** In 61857 from S.5548, Lower Miri Formation, × 3. a, dorsal view; b, right lateral view; c, anterior view.

Fig. 3 *Ampliura simplex* gen. et sp. nov. **Holotype** In 62157 from S.5537, Seria Formation, × 5. a, dorsal view; b, ventral view; c, right lateral view.

Fig. 4 *Nucia borneoensis* sp. nov. **Holotype** In 62145 from S.5548, Lower Miri Formation, × 4. a, dorsal view; b, anterior view; c, right lateral view.

Figs 5, 6 *Nucia borneoensis* sp. nov. Fig. 5, paratype In 62148 from S.10475, Lower Miri Formation, × 4. a, dorsal view; b, right lateral view. Fig. 6, ventral view of paratype In 62146 from S.5548, Lower Miri Formation, × 3.

Fig. 7a *Typilobus marginatus* sp. nov. Dorsal view of **holotype** In 62163 from NB 11541, Middle Miocene, Tungku Formation, × 3. See also Figs 7b–d (p. 14).



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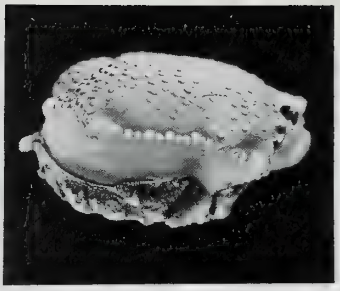

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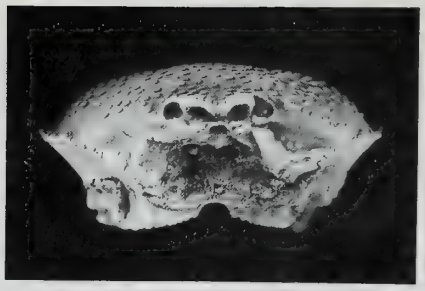

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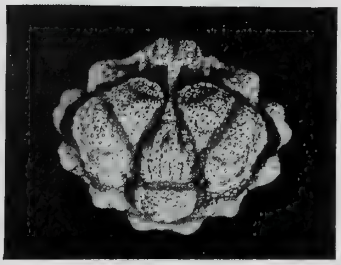

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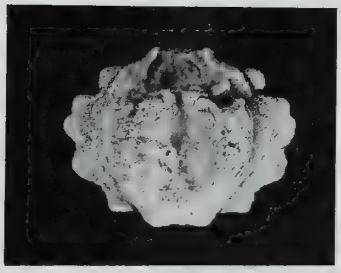

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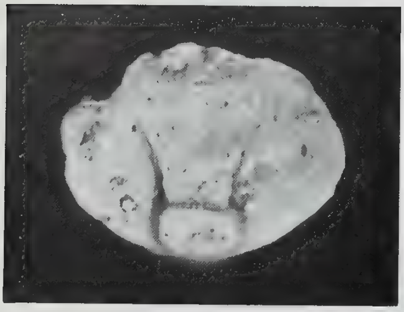

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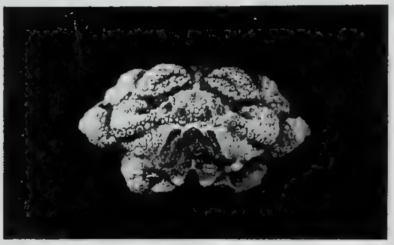

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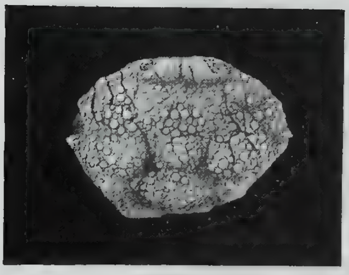

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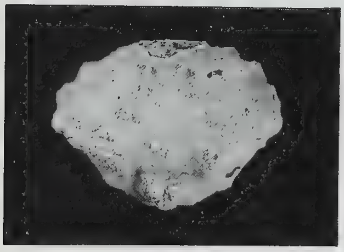

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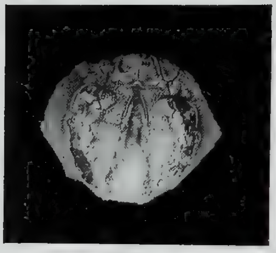

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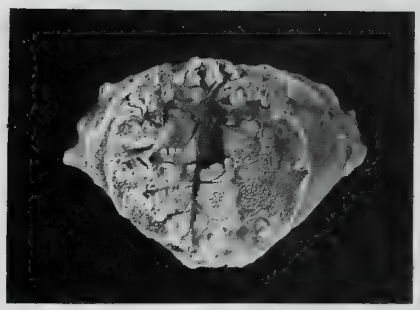

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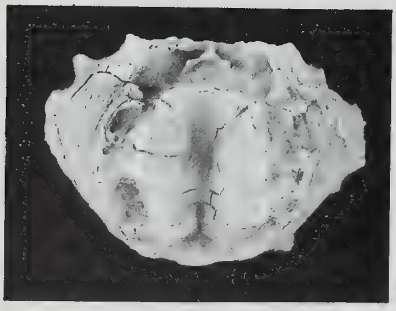

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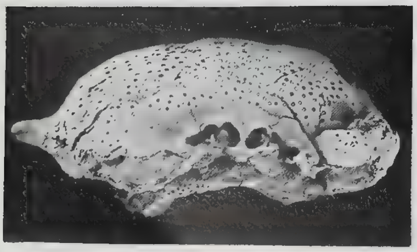

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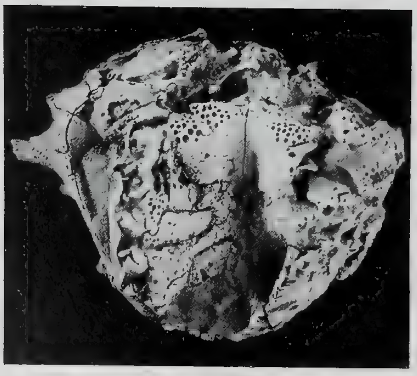

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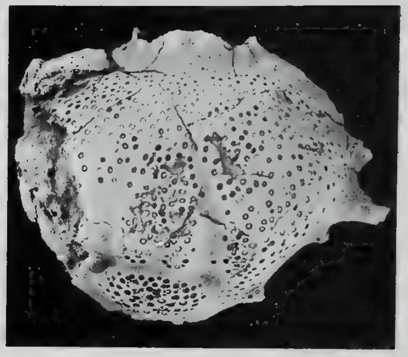

15a

Description. The carapace is rhomboidal in outline, about one-sixth longer than wide and much narrowed anteriorly. The front is moderately produced and the narrow triangular elevation above it is somewhat flattened and extends back a short distance. There is a very shallow depression either side of the front and the convex anterolateral margins are constricted again immediately before the broadly rounded lateral angles, set at some three-fifths the distance from the front. The margin is sharp and finely granulate, with the granules becoming sparser as they extend above the posterolateral margin as far as the posterior angles. The posterolateral margins converge to shallow incisions for the 5th coxae; the posterior margin is about twice the width of the front, nearly straight and bounded by a narrow, almost smooth ridge.

The thoracic sinus is very broad and ends in an obscure depression just in front of the first limb; there are a few minute granules scattered within the depression and a few others line its lower margin.

Internal moulds show low granular 'ridges' flanking an obscure median 'ridge' on the gastric region, and there is a group of three granules set in an inverted triangle on the cardiac region.

On the male abdomen somites 3–5 are fused and together equal the length of the 6th somite; the 3rd–5th somites of the female are very narrow, while the 6th occupies almost all the sternal area. In both sexes the telson is much reduced in size and extends well into the 3rd sternites.

Discussion. See below.

Leucosia tutongensis sp. nov. Fig. 24

Diagnosis. The carapace is rhomboidal with the front not much produced; the broad, shallow thoracic sinus terminates in a deep pit.

Name. 'From Tutong'.

Holotype. In 61885 (Figs 24a–c) from locality S.5539, Upper Miri Formation. Paratypes In 61886 from S.5544, Lower Miri Formation and In 61887–9 from S.5548, Lower Miri Formation.

Description. The carapace is similar in outline to *Leucosia serenei* but about one-fifth longer than wide. The front is not much produced and the triangular elevation above is rounded and extends a short distance back. There is a shallow depression on either side of the front and the weakly convex anterolateral margins lead to narrowly rounded lateral angles set at about mid-carapace length. From the lateral angle a minutely granulated ridge, continuous with the anterolateral margin, extends back onto the branchial region to about as far as the 3rd pair of limbs; the true posterolateral margin is finely granulate, weakly incised for the 5th limb and leads by way of acute posterior angles to the posterior margin which is straight to weakly convex and finely granulated.

The broad, rather shallow thoracic sinus ends in a deep ovate pit just in front of the insertion of the 1st limb; a few fine granules line the lower margin of the sulcus and there is a scattering of minute granules within the pit.

Deep wedge-shaped gonopores open into the abdominal cleft at the 5th sternites and are bounded behind by a narrow, wall-like process extending from the 6th sternites (Fig. 24c). The abdomen of the male is similar to that of *Leucosia serenei*.

Discussion of the species of *Leucosia*. The carapace width of *Leucosia longiangulata* sp. nov. is greater in relation to length than either *Leucosia serenei* sp. nov. or *Leucosia tutongensis* sp. nov.; it may be further distinguished by the elongate, forwardly situated lateral angle, by the deep thoracic sinus and the groove extending from it to the lateral edge. *L. longiangulata* compares well with *L. vittata* Stimpson, 1858, but the thoracic sinus is much further forward, hence the maximum width is also much further forward. It compares best with *L. serenei* sp. nov., but the thoracic sinus in the latter species does not reach the upper margin.

The subcarinate transverse section of *L. serenei* compares by and large with that of *Leucosia obscura* Bell, 1855, Recent of the Philippine Islands, but the latter species is a little broader with a narrow thoracic sinus terminating in a double notch, rather than broad and terminating in a depression as in *L. serenei*. *L. tutongensis* superficially resembles the Recent widespread Indo-Pacific *Leucosia longifrons* de Haan, 1841.

Genus ***MYRA*** Leach, 1817

Type species. By monotypy *Leucosia fugax* Fabricius, 1798 [ICZN Opinion 712]; from Recent of the Indo-Pacific Region.

Range. Miocene to Recent.

Myra brevisulcata sp. nov. Fig. 29

Diagnosis. The carapace is subovate with laterally developed shallow cervical furrows; the anterolateral margin is represented by a cluster, rather than a line, of granules; larger granules are scattered over an otherwise minutely granulated surface.

Name. 'With short furrows'

Holotype. In 61900 (Fig. 29) from locality S.10474, Lower Miri Formation.

Description. The carapace is subglobose with three moderately stout sharp spines, one at each posterior angle and a larger median one just above the posterior margin. The length excluding the spine slightly exceeds the breadth; it is widest at about midlength. Details of the slightly ascending front are not preserved. The outer wall of the hepatic region,

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Fig. 7b–d *Typilobus marginatus* sp. nov. **Holotype** In 62163 from NB 11541, Middle Miocene, Tungku Formation, × 3. b, ventral view; c, right lateral view; d, anterior view. See also Fig. 7a (p. 12).

Fig. 8 *Typilobus* sp. Dorsal view of abraded specimen In 46373 from NB 132, ?Lower Miocene, Simengaris Formation, × 6.

Fig. 9 *Drachiella guinotae* sp. nov. **Holotype** In 61863 from S.10475, Lower Miri Formation, × 2. a, dorsal view; b, ventral view; c, anterior view.

Fig. 10 *Nucia calculoides* sp. nov. **Holotype** In 62158 from S.10474, Lower Miri Formation, × 3.

Figs 11–14 *Iphiculus miriensis* sp. nov. Locality S.5548, Lower Miri Formation. Fig. 11, dorsal view of **holotype** (♂) In 62123, × 2. Fig. 12, ventral view of paratype (♀) In 62124, × 3. Fig. 13, ventral view of paratype (♂) In 62125. Fig. 14, ventral view of paratype (♂) In 62126, × 3.

Fig. 15 *Iphiculus granulatus* sp. nov. **Holotype** (♀) In 61868 from Penanjong, Seria Formation, × 3. a–c, dorsal, ventral and anterior views.

forming the apparent anterolateral margin, is well rounded, ridged and granulated with finer granules interspersed; it terminates in a shallow pit in which the granules are minute and confined to the upper posterior wall. A line of granules overlapping the ridge passes over the pit and continues back to form the posterolateral margin, which is sharp. Its demarcating line of granules becomes finer and runs back almost as far as the middle of the cardiac region and limits the upward extent of a densely granulated area. A low, rounded ridge with scattered granules, representing the anterolateral margin, extends between the front to above the marginal pit. The cervical furrows are present as broad lateral depressions curving forward round the foregoing ridge to become obsolete just above the anterior granules of the posterolateral margins.

A few scattered granules occur on an otherwise finely pitted dorsal surface.

DISCUSSION. The extension of the posterolateral margin over the marginal pit, laterally developed cervical furrows and sparsely granulated dorsal surface, together with the broadest part of the carapace occurring further back, readily distinguish this species from *Myra subcarinata* sp. nov. and *Myra trispinosa* sp. nov.

Myra subcarinata sp. nov. Fig. 27

DIAGNOSIS. The carapace is subovate and vaguely carinated; the median is the stoutest of the three posterior spines; the dorsal surface is finely granulated.

NAME. 'Slightly keeled'.

HOLOTYPE. In 61891 (Figs 27a–c) from locality S.5548, Lower Miri Formation. Paratype In 61892 from S.5539, Upper Miri Formation.

DESCRIPTION. The carapace is subglobose, obscurely carinated, with three stout, bluntly rounded spines, one at either angle of the posterior margin, and much the longest a median one just above the posterior margin. Exclusive of the spine, the length just exceeds the breadth. The slightly ascending orbitofrontal margin occupies about one-third of the width and the narrow triangular front is sulcate and downturned at its tip. Behind the orbital angle an angularly convex anterolateral margin is formed by the side wall of the subhepatic region which is continuous with the upper surface of the carapace and lined with a row of granules ending posteriorly in a shallow pit. Behind the pit the posterolateral margin is abruptly convex; it is sharp-edged and lined with granules for about half its length, after which the granules give way and the edge becomes rounded.

The regions are poorly defined. Behind the front, on either side of the midline is a shallow semi-circular depression. An exceedingly fine groove lined with pits separates the cardiac from the gastric regions and shallow depressions, rather than furrows, separate the anterior half of the cardiac from the branchial region.

A little above and anterior to the marginal pit is a granule somewhat larger than those crowding the dorsal surface; the latter tend to form a straggling median line extending to the front. The granules beneath the hepatic lobe and those lining either side of the marginal pit are more variable in size.

DISCUSSION. The shorter, less excavated anterolateral margin and partially granulated posterolateral margin distinguish this species from *M. fugax*.

Myra trispinosa sp. nov. Fig. 28

DIAGNOSIS. The carapace is subovate with three stout posterior spines of which the median is the longest; the anterolateral margins are marked by a line of granules.

NAME. 'Three-spined'.

HOLOTYPE. In 61893 (Figs 28a–c) and paratypes In 61894–5, all from locality S.5548, Lower Miri Formation. Paratypes In 61896–7, from S.5539, Upper Miri Formation; paratypes In 61898–9 from S.5544, Lower Miri Formation.

DESCRIPTION. A large subglobose species with three stout, bluntly rounded spines, one at each posterior angle and a larger median one just above the posterior margin. The length, excluding spine, slightly exceeds the breadth. Details of the front are not preserved. Behind the orbital angle and above the apparent anterolateral margin formed by the outer wall of the sub-hepatic region, the true margin is represented by a short row of granules. The granules lining the hepatic margin become clustered posteriorly and the margin ends in a shallow pit. The posterolateral margin commences above the pit and its sharp, granulated edge extends almost to the posterior margin.

The regions are poorly defined. The anterior wall of the marginal pit is granulated and over the dorsal surface there is a scattering of larger granules among densely crowded minute granules. A subsurface shell layer shows a similar arrangement of pits.

DISCUSSION. *Myra trispinosa* sp. nov. is distinguishable from *M. subcarinata* by the presence of granules forming the anterolateral margin, the posterolateral margin commencing above the marginal pit, and the continued sharp edge of that margin posteriorly.

Genus ***NUCIA*** Dana, 1852

TYPE SPECIES. By monotypy *Nucia speciosa* Dana, 1852, from Recent of Indo-Pacific.

Figs 16, 18 *Iphiculus granulatus* sp. nov. Paratype (♂) In 61869 from Penanjong, Seria Formation, × 3. Fig. 16, dorsal view; Fig. 18, ventral view.

Fig. 17 *Iphiculus sexspinosus* sp. nov. **Holotype** In 61864 from S.5536, Seria Formation, × 2. a, dorsal view; b, ventral view.

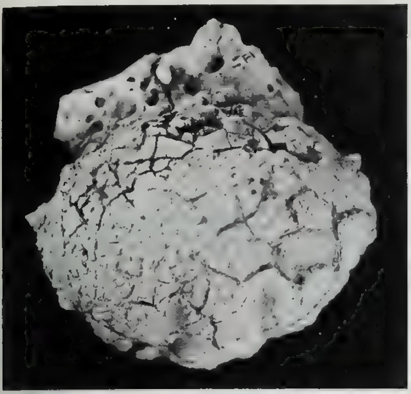
Fig. 19 *Iphiculus sexspinosus* sp. nov. Latex cast of paratype In 61865 from S.5539, Upper Miri Formation, × 2.

Figs 20–23 *Leucosia serenei* sp. nov. from S.5548, Lower Miri Formation. Fig. 20, **holotype** In 61870, × 3. a, b dorsal and right lateral views. Fig. 21, paratype (♂) In 61871, ventral view, × 4. Fig. 22, paratype (♀) In 61872, ventral view, × 3. Fig. 23, paratype (♀) In 61873, ventral view showing the gonopores, × 3.

Fig. 24 *Leucosia tutongensis* sp. nov. **Holotype** (♂) In 61885 from S.5539, Lower Miri Formation, × 3. a, dorsal view; b, ventral view; c, right lateral view showing the gonopores.

Figs 25, 26 *Leucosia longiangulata* sp. nov. **Holotype** In 61890 from S.10474, Lower Miri Formation, × 3. Fig. 25, dorsal view; Fig. 26, right lateral view.

Fig. 27 *Myra subcarinata* sp. nov. **Holotype** In 61891 from S.5548, Lower Miri Formation, × 2. a–c, dorsal, right lateral and anterior views.



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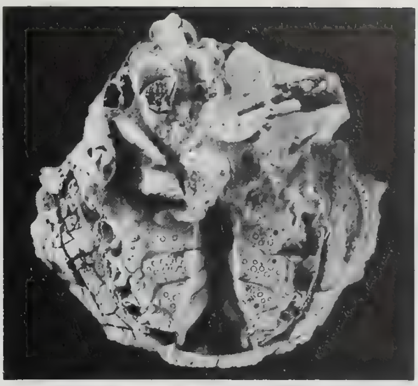

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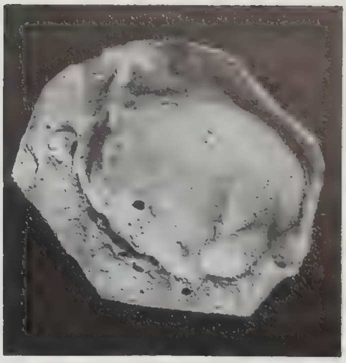

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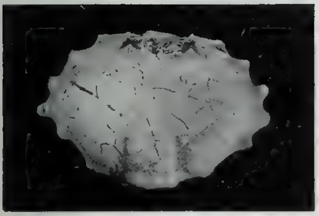

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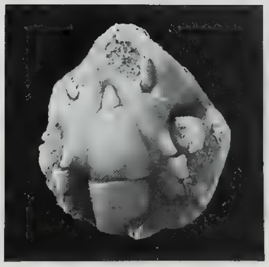

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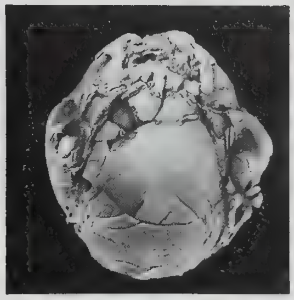

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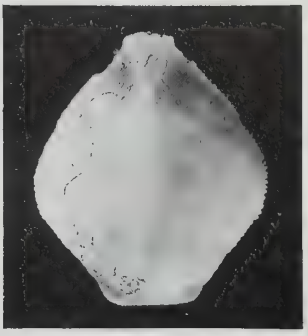

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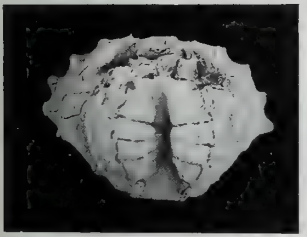

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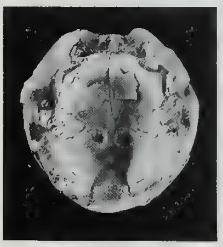

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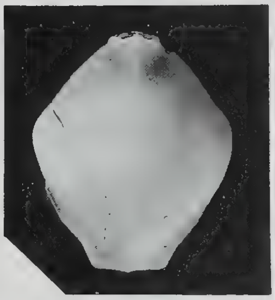

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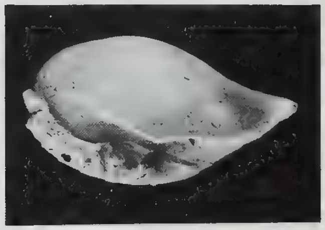

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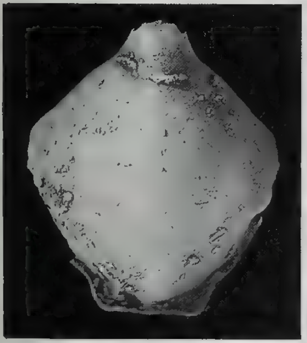

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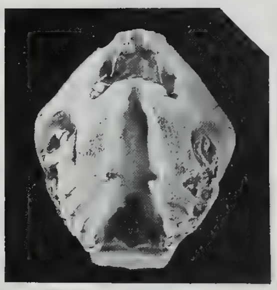

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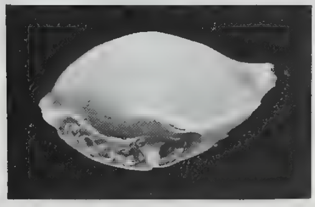

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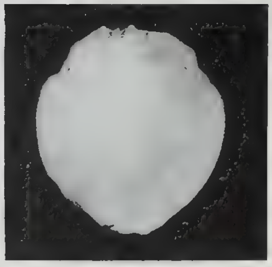

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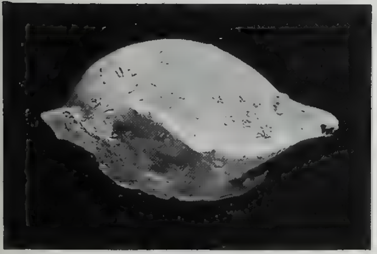

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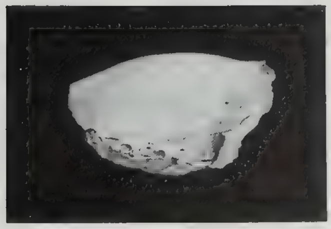

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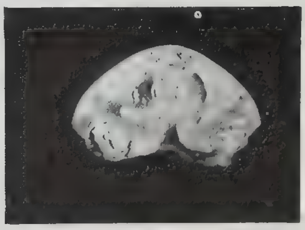

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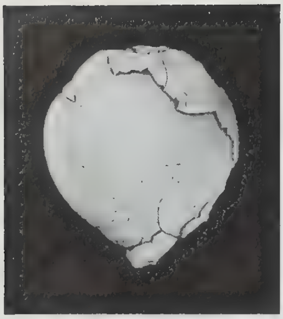

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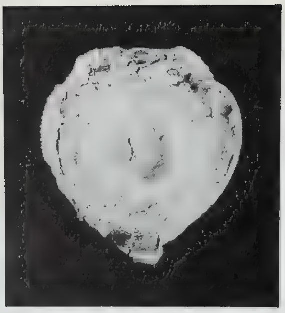

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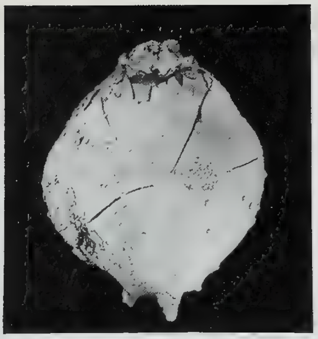

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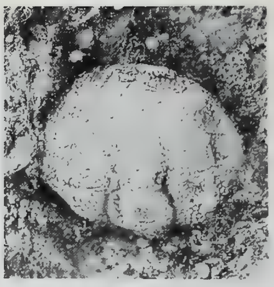

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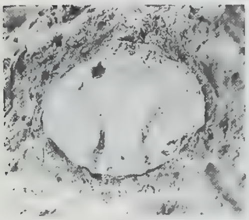

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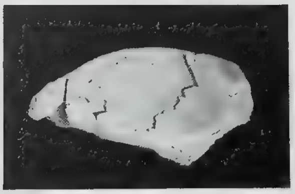

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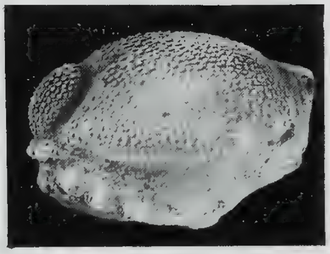

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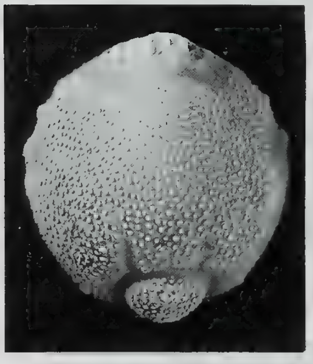

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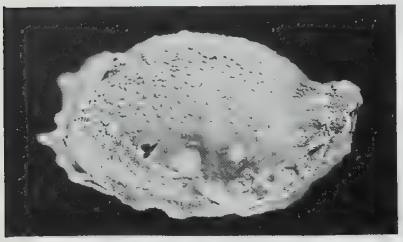

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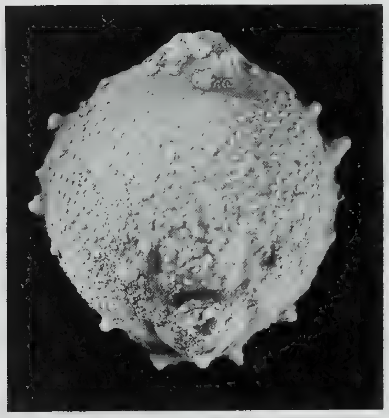

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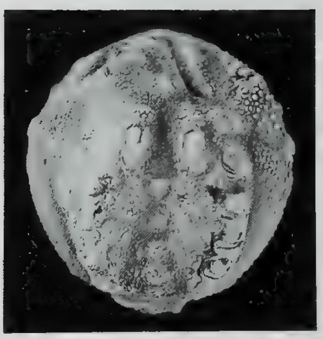

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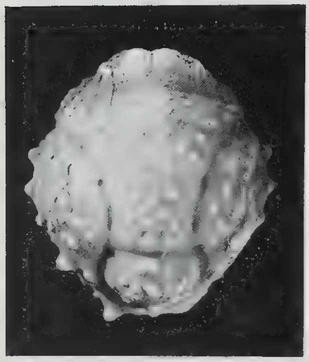

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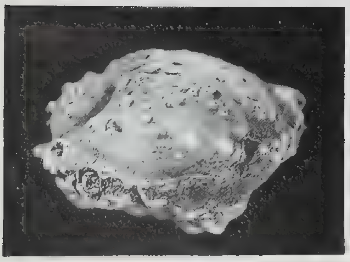

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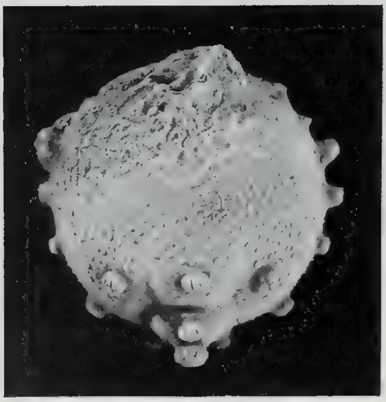

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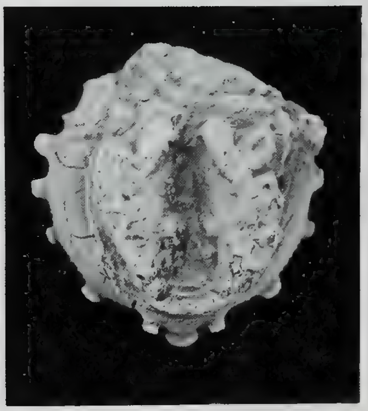

35b

Range. Miocene to Recent.

Nucia borneoensis sp. nov. Figs 4–6

Diagnosis. The carapace is subovate with a spine at the lateral angle and one on the posterolateral margin; the furrows are fully, but shallowly, developed and the dorsal surface is coarsely granulated.

Name. 'From Borneo.'

Holotype. In 62145 (Figs 4a–c), and paratypes In 62146 (Fig. 6), In 62147 from locality S.5548; paratypes In 62148 (Figs 5a, b), In 62149 from S.10475; paratypes In 62151–6 from S.5550. All from Lower Miri Formation.

Description. The carapace is transverely subovate, rather more steeply arched longitudinally than transversely. There is a sharp spine at the lateral angle, another opposite the base of the cardiac region and a small one at each corner of the intestinal region. The orbitofrontal margin occupies about half the carapace width and the circular orbits are distinctly divided by a septum from ovate antennular fossae. The broadly triangular front is steeply downturned and weakly sulcate, the sulcus extending back to a postfrontal ridge. In plan view the frontal margin is nearly straight, slightly indented at the midline.

With the exception of the well-developed furrows, which are finely and evenly granulated, the dorsal surface is densely covered with coarse granules of several diameters.

The groove above the pterygostomian process is thin and smooth, the pterygostomian region itelf is elongate, granulated and just sufficiently inflated to be level with the anterolateral margin when viewed from above.

The abdominal sternites are nearly flat on either side of the deep abdominal trough; the 4th sternites are subrectangular and about twice the length of the 5th; the 6th–8th sternites diminish in size posteriorly.

Discussion. See p. 20.

Nucia calculoides sp. nov. Fig. 10

Diagnosis. The carapace is almost circular in outline, the anterolateral indentation is weak and the lateral spines are only feebly developed; the entire dorsal surface is covered by flattened granules.

Name. Referring to the pebble-like surface ornament.

Holotype. In 62158 (Fig. 10) from locality S.10474, Lower Miri Formation. Paratypes In 62159–62 from S.5544, Lower Miri Formation.

Description. The carapace is almost circular in outline and moderately curved transversely. Longitudinally it is evenly curved after a shallow postfrontal depression. The anterolateral margins are convex to a shallow indentation at the cervical notch, then straight as far as a feeble spine, hardly bigger than the granules lining the edge of the margin. The posterolateral margins are slightly convex and there is no definite spine near the narrowly rounded posterior angle. The slightly convex posterior margin is about as wide as the orbitofrontal margin, which is rather less than half the carapace width; the front is a little produced, downturned and broadly sulcate. Viewed from above the frontal edge runs back on either side of a fine median notch dividing round the tip of the anterior mesogastric process. Fine granules line the frontal and orbital margins.

The grooves bounding the regions are thin, but sharply defined. The hepatic regions are clearly differentiated and the subcircular cardiac region is barely elevated above the general surface curvature.

Within the postfrontal depression there is a tendency for fine granules to form concave rows behind the orbits and affect the outline of the protogastric lobes. Behind, the dorsal surface is crowded with flattened granules interspersed with fine granules, and granules of varying size crowd the bottoms of the grooves. Similar granules crowd the elongate, rather subdued pterygostomian region as well as the groove above it and the branchiostegites.

Details of the ventral surface are not well preserved, but the abdominal trough extends to the tip of the 4th sternites, which are trapezoidal in outline and rather more coarsely granulate than the succeeding sternites.

Discussion. See p. 20.

Nucia coxi sp. nov. Figs 30, 31

1954	*Nucia* sp. Cox *in* Collenette: 15.
1954	*Nucia* sp. (probably *N. Fennemai* Böhm): Cox *in* Collenette: 15.

Diagnosis. Carapace subcircular, with three lateral spines and a spine at the posterolateral angle. Cervical groove broad but shallow, becoming almost imperceptible at the midline. Dorsal surface covered with even-sized granules.

Name. In honour of the late Dr L.R. Cox.

Holotype. In 62164 (Fig. 30) from locality J 771, (?Lower) Miocene. Paratype In 46375 (Fig. 31) from locality NB 130, ?Lower Miocene.

Description. The carapace is rounded in outline, somewhat broader than long; longitudinally and transversely it is gently convex. The lateral spines are not well preserved, but basal scars indicate one on the posterolateral margin behind the marginal notch, one opposite the base of the cardiac region and another equidistant between them. The spines at the posterior angles are poorly developed. The cervical furrow is broad, but shallow as it curves gently down from the marginal notch and becomes almost imperceptible where it crosses the

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Fig. 28 *Myra trispinosa* sp. nov. **Holotype** In 61893 from S.5548, Lower Miri Formation, × 1.5. a–c, dorsal, ventral and right lateral views.

Fig. 29 *Myra brevisulcata* sp. nov. **Holotype** In 61900 from S.10474, Lower Miri Formation, × 2.

Figs 30, 31 *Nucia coxi* sp. nov. Fig. 30, **holotype** In 62164 from J.771, ?Lower Miocene, × 4. Fig. 31, paratype In 46375 from NB 130, ?Lower Miocene, × 3.

Fig. 32 *Pariphiculus gselli beetsi* subsp. nov. **Holotype** In 61901 from S.5539, Lower Miri Formation, × 4. a–c, dorsal, right lateral and ventral views.

Fig. 33 *Pariphiculus papillosus* sp. nov. **Holotype** In 61902 from S.10474, Lower Miri Formation, × 3. a, b, dorsal and right lateral views.

Fig. 34 *Nucilobus symmetricus* gen. et sp. nov. **Holotype** In 61903 from S.5549, Lower Miri Formation, × 4. a, b, dorsal and right lateral views.

Fig. 35a, b *Pariphiculus verrucosus* sp. nov. **Holotype** In 61904 from S.10475, Lower Miri Formation, × 3. a, b, dorsal and ventral views. See also Fig. 35c (p. 22).

midline; it is joined by fine, very short, straight hepatic furrows. On each protogastric lobe an obscure ridge (more noticeable on an internal mould) runs parallel to the cervical furrow amd has a node at the posterior end; similar-sized nodes occur close to the midline on the urogastric lobe. Deep furrows separate the urogastric lobe and cardiac region from one another and from the branchial regions. The tumid, rounded-pentagonal cardiac region does not overhang the posterior margin; a narrow median tongue extends into the urogastric lobe. The dorsal surface is densely crowded with more or less even-sized granules.

DISCUSSION of species of *Nucia*. There is a noticeable difference in the length/width ratios between *N. borneoensis* and *N. calculoides*, the latter being rather wider in relation to length. It differs also in having the cardiac region wider than the base of the mesogastric lobe and ovate rather than rounded as in *N. borneoensis*; the primary granules on *N. borneoensis* are more widely dispersed and hemispherical rather than being densely packed and flattened as they are in *N. calculoides*.

The weak lateral extension of the cervical furrow and hepatic furrows, together with the finer, denser granulation, distinguishes *N. coxi* from the foregoing species. *N. baripadensis* Bachmayer & Mohanti, 1973 (Miocene, eastern India) is rather similar in outline to *N. coxi* but has a sharper indentation in the anterolateral margin; the anterior portions of the furrows are as weakly developed and the cardiac region of the Indian species appears to be more ovate; its surface ornament consists of numerous cratered pits – possibly the ornament of a sub-surface shell layer.

Of Recent species, the type species *N. speciosa* differs in having a rather more protruding front and areolated lobes which obscure the lateral extension of the cervical and hepatic furrows, but it has well-defined median gastric and cardiac lobes in common with *N. borneoensis* and *N. calculoides*. *Nucia tuberculosa* Milne Edwards, 1874 and *Nucia perlata* Sakai, 1965 have a rounded carapace with subdued marginal spines; the latter has well-defined hepatic and frontal lobes.

Nucia fennemai Böhm, 1922, from the ?Lower Miocene of Java (l/w = 0.8) is relatively broader than *N. coxi*, which has a l/w ratio of 0.9. Otherwise they are very similar; they each have three lateral spines and a posterolateral spine. *N. coxi* differs in that it has a wider front, the cervical groove is more strongly impressed and the dorsal surface is covered with densely crowded even-sized granules. The granules on the dorsal surface of *N. fennemai* are not so dense and become much more widely spaced on the branchial regions. *N. fennemai* is relatively narrower than both *N. borneoensis* (l/w = 0.75) and *N. calculoides* (l/w = 0.65). Both *N. borneoensis* and *N. calculoides* have much coarser ornament and that of *N. calculoides* is pebble-like.

Genus ***NUCILOBUS*** nov.

TYPE SPECIES. *Nucilobus symmetricus* sp. nov.

DIAGNOSIS. Carapace longer than broad, subovate with five small marginal tubercles. The cervical furrow is shallow medially, but has deep anterolateral extensions to the margin; it is continuous with a furrow delimiting the urogastric and cardiac regions. Hepatic furrows present. The dorsal surface has a tubercular ornamentation and there are three pairs of pits in the cervical/urocardiac furrows.

NAME. Varied from *Nucia*. Masculine.

Nucilobus symmetricus gen. et sp. nov. Fig. 34

DIAGNOSIS. As for genus.

NAME. 'Symmetrical', from the bilateral arrangement of the surface ornament.

HOLOTYPE. A female, In 61903 (Figs 34a, b) from locality S.5549, Lower Miri Formation.

DESCRIPTION. The carapace is subovate in outline, a little longer than wide and widest at about midlength. The anterolateral margins are slightly constricted, both behind the orbits and before the cervical notch; they are short and lined with 4 or 5 granules. Behind the cervical notch a very small tubercle is followed by four evenly-spaced larger ones; the fourth, set opposite the cardiac region, is followed by another one at the posterior angle. The orbitofrontal margin occupies half the carapace width. It is not produced and is directed almost straight forward; viewed from the side the curvature is only a little less than the general longitudinal curvature of the carapace. The front is wide, steeply downturned into an acutely triangular rostrum, and a deep median sulcus bifurcates, with each branch partially encircling a 'frontal lobe'.

The cervical furrow is deep from the lateral margin to the outer angle of the mesogastric lobe, but becomes very faint where it crosses the midline; anteriorly weak furrows partly separate the hepatic regions from the protogastric lobes. Deep grooves separate the rather large subquadrate urogastric lobe from the cardiac region and the cardiac from the intestinal and branchial regions. The tumid, rounded-pentagonal cardiac region does not overhang the posterior margin and is about as wide as the intestinal region, on which the corner tubercles are somewhat more spiny than the marginal ones.

There is a pit at the junction of the cervical and hepatic furrows, one at the outer angle of the urogastric and another midway along that lobe. A row of four granules lining the anterior border of the urogastric lobe is followed by six granules encircling a median one. Granules forming an outer ring on the cardiac region enclose two larger ones and the remaining surface is sparsely ornamented by granules of several diameters bilaterally distributed in semicircular or linear patterns.

The pterygostomian region is very narrow and lined with granules extending beyond the anterolateral margin.

DISCUSSION. In having anterolaterally developed cervical furrows and hepatic furrows *Nucilobus symmetricus* has elements in common with *Nucia* – particularly the new forms *N. borneoensis* (p. 19) and *N. calculoides* (p. 19) described above. The new genus differs from *Nucia*, however, in being much longer than broad and in the presence of the furrow pits (although *Nucia speciosa* appears to have two pairs: one at the broadest part of the mesogastric lobe and one midlength of urogastric lobe). *Pariphiculus* (p. 21) has a similarly elongate carapace, but lacks the prominent grooves. This suggests a lineage from *Nucilobus* to *Pariphiculus* through a reduction in carapace grooves, especially the cervical groove which in *Pariphiculus* is seen only as an anterolateral notch.

Genus *PARIPHICULUS* Alcock, 1896

Type species. By subsequent designation of Rathbun, 1922: *Randallia coronata* Alcock & Anderson, 1894 [ICZN Opinion 73]; from Recent of the Bay of Bengal.

Range. Middle Miocene to Recent.

Pariphiculus gselli Beets ***beetsi*** ssp. nov. Fig. 32

Diagnosis. Narrow (*trans.*) intestinal region with extra tubercle at the posterolateral limit of the metabranchial region. Cardiac tubercles and pair of tubercles parallel to the branchiocardic groove obsolete.

Name. In honour of Dr C. Beets.

Holotype. In 61901 (Figs 32a–c) from locality S.5539, Lower Miri Formation.

Description. The carapace is small, subglobose and subcircular in outline; the length slightly exceeds the breadth. Of the four tubercular processes on the anterolateral margin, the 1st and 2nd are hardly more than enlargements of the granules forming the surface ornament; the 4th, the largest, occurs at the widest part of the carapace and is followed immediately by another tubercle and one, much reduced, lies opposite the cardiac region. The orbitofrontal margin, occupying about a third of the carapace width, is only a little produced and barely upturned; the very small, acutely triangular rostrum is sharply downturned and a low, sinuous ridge borders the frontal margin.

The basal portion of the mesogastric region is defined by faint furrows which rapidly deepen posteriorly and delimit the urogastric and cardiac regions. The bulbous, almost circular cardiac region overhangs the posterior margin; it has two obscure, even-sized granules in line medially and is wider than the short intestinal region on which the corner tubercles are similar to the larger-sized lateral ones.

A narrow postfrontal area is only sparsely granulated, but the remainder of the dorsal surface is densely and finely granulated, the granules becoming a little coarser towards the metabranchial lobes. A row of granules, becoming sparser and finer posteriorly, borders the pleural suture. The pterygostomian region is weakly tumid and granulated; when viewed from above, a small tubercle at its centre is clearly visible beyond the lateral margin.

The abdominal sternites are shallowly depressed, more or less rectangular in outline and decrease in size posteriorly.

Discussion. The new subspecies differs from the nominal subspecies (Beets 1950) from the Rembangian (Tf_2) of Java only by the absence of the pair of tubercles on the metabranchial region parallel to the cervical groove and the absence of the single tubercle on the urogastric region. It also differs from *Pariphiculus coronatus* (Alcock & Anderson, 1894) from the Recent of the Bay of Bengal by the absence of the same tubercles, but *P. gselli beetsi* subsp. nov. is relatively wider. *Pariphiculus rostratus* Alcock, 1896 from the Recent of the Malabar Coast differs from *P. g. beetsi* because in *P. rostratus* the cardiac tubercles have become extended into spines.

Pariphiculus papillosus sp. nov. Fig. 33

Diagnosis. The carapace is subovate, slightly longer than broad, with six small marginal tubercles; the larger, hindmost tubercle on the cardiac region barely overlaps the posterior margin; the dorsal surface is densely granulated.

Name. From the papillate nature of the marginal spines.

Holotype. In 61902 (Figs 33a, b) from locality S.10474, Lower Miri Formation.

Description. The carapace is subglobose and subovate in outline, only a little longer than broad with the greatest width occurring at about midlength. On the anterolateral margins are four small, nipple-like tubercles of which the first is much reduced in size; of two similar tubercles on the posterolateral margins, the first is very small and the second lies opposite the hinder, larger tubercle on the cardiac region. The posterior margin is about as wide as the frontal border. The orbitofrontal margin is directed a little upwards; the front takes up the middle third and the slightly produced, acutely triangular rostrum is downturned at its tip. The upper orbital margin is thin and deeply pierced by two notches.

Apart from the furrows delineating the basal part of the urogastric lobe and cardiac region, the lobes are undifferentiated. The bulbous, almost circular cardiac region has two tubercles, the hindmost of which barely overlaps the posterior margin. The short intestinal is as wide as the cardiac and the spine above each corner is finer and more attenuated than those on the lateral margins. There is a small tubercle on each metabranchial lobe close to the intestinal lobe.

With the exception of a narrow postfrontal area and a narrow strip above the 2nd–4th lateral tubercles, the dorsal surface is covered with densely crowded granules of more or less even size.

The lateral edges are rounded and the pterygostomian region is sparsely granulated.

Discussion. This species differs from all other *Pariphiculus* by the papillate nature of the marginal spines.

Pariphiculus verrucosus sp. nov. Fig. 35

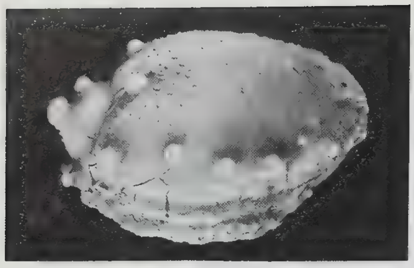
Diagnosis. The carapace is broadly ovate with four warty tubercles on the lateral margins; the dorsal surface is granulated and has seven tubercles, of which the hindmost one on the cardiac region clearly overhangs the posterior margin.

Name. 'Warty', from the appearance of the tubercles.

Holotype. In 61904 (Figs 35a–c) from locality S.10475, Lower Miri Formation.

Description. The carapace is similar in outline to the previous species but widest at the anterior third. There are several granules decreasing in size on the short, convex anterolateral margins; a longer, warty tubercle occurs immediately after an obscure cervical notch, and is followed on the convex posterolateral margin by three other tubercles of which the second is somewhat smaller.

The orbitofrontal margin is damaged in the holotype, but appears to have been only a little upturned. The urogastric lobe and the cardiac and intestinal regions are separated from one another and from the branchial regions by deep grooves. When viewed from the side the subpentagonal cardiac, and to a lesser extent the narrow, bar-like intestinal regions, overlap the posterior margin. The bottoms of the furrows are smooth and except for the cardiac and intestinal regions, which are minutely granulated, the dorsal surface is crowded with coarse granules of several diameters. There are, in addition,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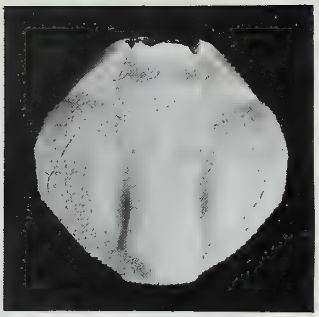
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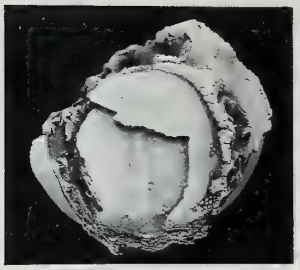
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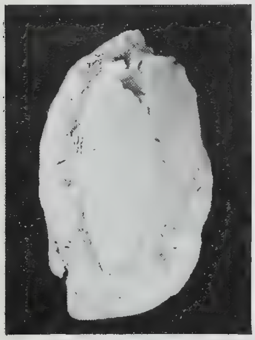
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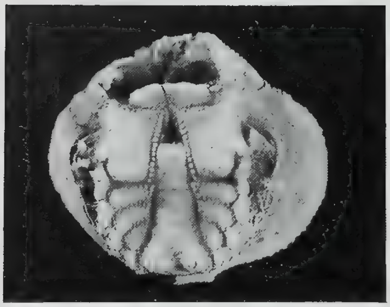
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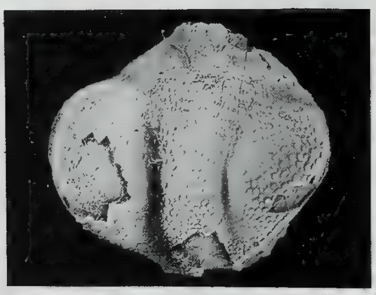
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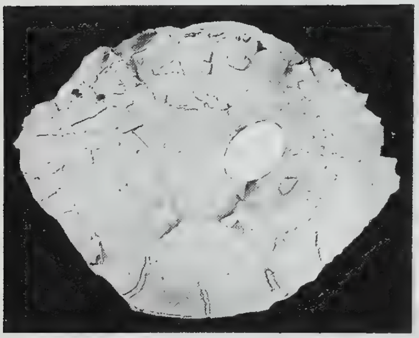
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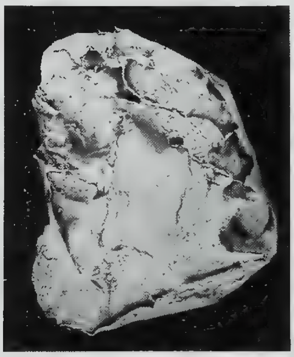
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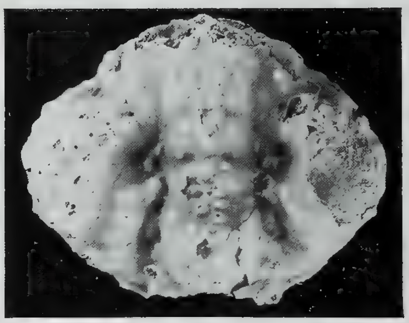
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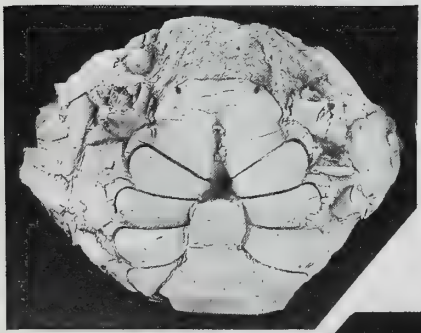
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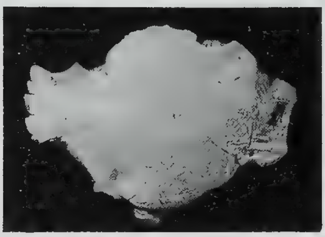
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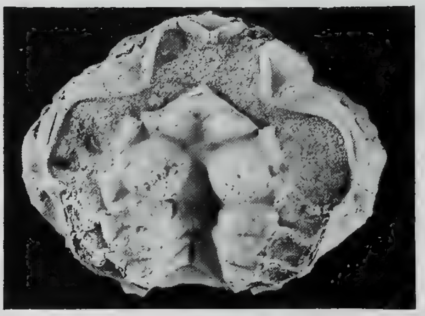
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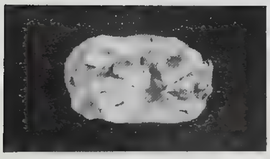
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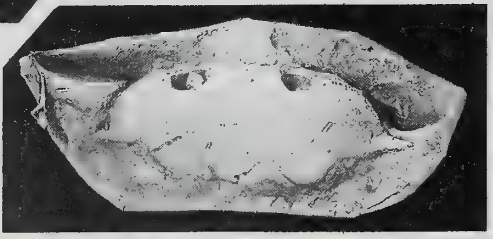
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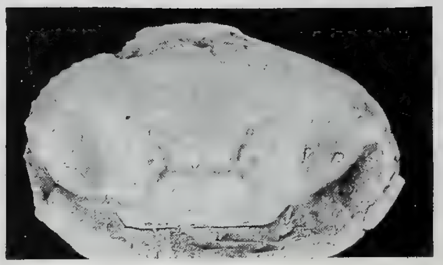
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seven warty tubercles: one on the urogastric lobe; two, the foremost of which is smaller, on the cardiac region; one on each metabranchial lobe; and one at each corner of the intestinal region.

The sides are inclined a little inwards and the slightly tumid pterygostomian region has a tubercle clearly visible when viewed from above.

Discussion. In the wart-like marginal and dorsal tubercles *P. verrucosus* has a marked affinity to *Pariphiculus agariciferus* Ihle, 1918, a Recent species from Roti Island (type locality) near Timor and Japan, but the latter species has additional tubercles on the gastric region, a much coarser surface granulation and poorly-defined grooves delimiting the regions.

Genus *PHILYRA* Leach, 1817

Type species. By subsequent designation of H. Milne Edwards, 1837: *Cancer globus* Fabricius, 1775 [ICZN Opinion 712]; from Recent of West Africa.

Range. Pliocene to Recent.

Philyra granulosa sp. nov. Figs 36–38

Diagnosis. Carapace octagonal with an entire lateral margin, post-frontal depression shallow; dorsal surface densely granulated.

Name. 'Granulated'.

Holotype. In 61905 (Fig. 36), and paratypes In 61906 (Figs 37a, b), In 61907 (Fig. 38), In 61908–10 from locality S.5548, Lower Miri Formation. Paratypes In 61911–2 from S.5538, Upper Miri Formation; In 61913–4 from S.5549, Lower Miri Formation.

Description. The subpyriform carapace is a little longer than wide; in side view the front is a little upturned with a shallow postfrontal depression. The anterolateral margins are short, straight to slightly convex, and the beaded edge surrounding the margin is not interrupted where the lateral extension of the cervical furrow reaches the edge. The posterior margin is as wide as the orbitofrontal margin, which occupies about half the carapace width. The front is wide, triangular, steeply downturned and broadly sulcate above. The orbits are directed slightly upwards and of the two fine fissures in the upper margins, the outermost lies close to the beaded edge.

Broad furrows separate the median gastric from the branchial regions and there is a small median incursion of the straight-sided cardiac region into the urogastric lobe; the rounded base of the cardiac region is confluent with a small, circular intestinal region. The hepatic regions are weakly tumid; deep subhepatic regions are inclined almost at right angles to the margin, and an almost smooth, flattened upper part is divided from a narrow, tumid lower part by a line of granules diverging from the marginal ones.

Numerous granules crowd the dorsal surface, although in some specimens the postfrontal depression is almost smooth; there is a denser, finer mass on either side of the cardiac region and a tendency for those on the branchial region to become coarser laterally.

In the male the 1st and 2nd sternites form a narrow triangular strip steeply inclined into the body cavity anteriorly and posteriorly sending back a narrow tongue separating the 3rd sternites. The 3rd sternites are subrectangular with a sinuous anterior border and a contra-sinuous posterior border; the subrectangular 4th sternites are wider than the 3rd and longer than the 5th–7th sternites, which become smaller and progressively more chordate posteriorly. The 4th sternites are granulated; the other sternites are relatively smooth and the abdominal trough is lined with beaded granules.

On specimen In 61906 (Figs 37a, b), a large bopyriform swelling occupies the entire left-hand branchial region.

Discussion. The evenly rounded transverse section and coarsely granulated dorsal surface most readily distinguish this species; *Philyra adamsii* Bell, 1855 has granules restricted to the posterior half of the carapace, while *P. pisum* de Haan, 1841, *P. carinata* Bell, 1855 and *P. kanekoi* Sakai, 1934, all have regionally distributed granules and all have a weak median carina.

Genus *TYPILOBUS* Stoliczka, 1871

Type species. By monotypy *Typilobus granulosus* Stoliczka, 1871 from the Lower Miocene of Sind, India.

Range. Middle Eocene to Middle Miocene.

Typilobus marginatus sp. nov. Fig. 7

Diagnosis. A large, transversely ovate carapace with very thin and granulated anterolateral edge.

Fig. 35c *Pariphiculus verrucosus* sp. nov. Right lateral view of **holotype** In 61904 from S.10475, Lower Miri Formation, × 3. See also Figs 35a, b (p. 18).

Figs 36–38 *Philyra granulosa* sp. nov. From S.5548, Lower Miri Formation, × 4. Fig. 36, dorsal view of **holotype** In 61905. Fig. 37, paratype (♂) In 61906. a, b, dorsal and ventral views of male with bopyriform swelling of left branchial chamber. Fig. 38, ventral view of paratype (♀) In 61907.

Fig. 39 *Raninoides* sp. In 61915 from S.5539, Lower Miri Formation, × 2.

Fig. 40 *Parthenope (Rhinolambrus) sublitoralis* sp. nov. **Holotype** In 61917 from S.5548, Lower Miri Formation, × 3. a, b, dorsal and ventral views.

Figs 41, 42 *Charybdis (Charybdis) feriata* (Linn.) *bruneiensis* subsp. nov. from S.4965, ?late Middle Pleistocene. Fig. 41, **holotype** In 59015. a, b, dorsal and ventral views, ×1; c, latex cast from external mould to show anterolateral spines, × 2. Fig. 42, dorsal view of paratype In 59012 from S.4918, ?late Middle Pleistocene, × 2.

Figs 43–45 *Portunus obvallatus* sp. nov. from S.5539, Upper Miri Formation. Fig. 43, dorsal view of **holotype** In 61947, × 3. Fig. 44, ventral view of paratype In 61948, × 2. Fig. 45, latex cast from external mould of paratype In 61949, × 3.

NAME. Referring to the sharp lateral margin.

HOLOTYPE. In 62163 (Figs 7a–d) from locality NB 11541, Tungku Formation, Middle Miocene.

DESCRIPTION. The length of the transversely oval carapace is about four-fifths of the breadth measured immediately in front of the lateral spines; it is moderately arched transversely and longitudinally flatly arched behind a weak postfrontal depression. The anterolateral margins are convex with hardly any indentation at the cervical notch. The spine at the lateral angle is set a little behind the mid-carapace length. It is bluntly rounded and upturned, and anteriorly it tapers into a very thin edge lined with granules. At the cervical notch the ridge divides; the stronger, lower branch is interrupted by a large cluster of granules on the pterygostomian region and terminates in a small tubercle beneath the orbit, while the upper branch continues to the upper orbital margin. The posterolateral margins are nearly straight with a small, wart-like tubercle opposite the widest part of the cardiac region. A similar tubercle occurs at the posterior angle and the posterior margin is about as wide as the orbitofrontal margin. The orbitofrontal margin occupies a third of the carapace width and the sides of the barely projecting front are feebly inclined to a shallow median depression. The frontal edge is lined with two or three rows of fine granules, giving way to smaller ones lining the upper orbital margin. The small orbits are rounded, the antennar fossae obliquely ovate.

The marginal parts of the cervical and hepatic furrows are barely discernible. Weak depressions separate the urogastric from the mesobranchial lobes. The pentagonal cardiac region is tumid and separated by broad grooves from the branchial regions and bounded behind by a narrow, flattened area from the posterior margin.

With the exception of a narrow beaded strip bordering the anterolateral margins and the bottom of the furrows, the dorsal surface is densely covered with small granules of several diameters.

The pterygostomian region is subtriangular, granulate and projects beyond the anterolateral margin. There are a few small granules beneath the lateral spine.

On the ventral surface the sternites are covered with granules decreasing in size posteriorly and each pair of sternites is bordered by a row of fine granules. The 4th sternites are trapezoidal in outline and about twice as long as the 5th; the 5th and 6th pairs are subrectangular and the 7th and 8th are chordate; the outer posterior angle of the 4th–6th pairs is directed backwards. The very deep abdominal trough extends well beyond the 4th sternites and is rimmed by a row of coarse granules.

DISCUSSION. This species differs from *T. granulosus* by the sharp granulose lateral margin, the smooth band on the branchial regions parallel to the lateral margin, and the two or three rows of granules lining the frontal edge. We agree with Dr P. Müller (*in litt.* 6/12/1987) that *Nucia baripadensis* Bachmayer & Mohanti, 1973 is probably the same as *T. granulosus*.

Typilobus sp. Fig. 8

MATERIAL. An abraded internal mould In 46373 (Fig. 8). Locality NB 132, ?Lower Miocene Te$_5$–f, Simengaris Formation (Silimpopon horizon of Wenk, 1938). South-east part of Silimpopon area, Tawau, Cowie Harbour, Sabah.

REMARKS. In view of the characters so well preserved on the foregoing species, it would seem unwise to give a specific name to this rather poorly preserved specimen. The outline of the carapace, together with the low flattened profile and the thin lateral edge, are strongly reminiscent of *T. marginatus* sp. nov.

Section **THORACOTREMATA** Guinot, 1977

Superfamily **GRAPSOIDEA** Macleay, 1838

Family **GRAPSIDAE** Macleay, 1838

Genus ***PALAEOGRAPSUS*** Bittner, 1875

TYPE SPECIES. By subsequent designation of Glaessner, 1929: *Palaeograpsus inflatus* Bittner, 1875, from Upper Eocene of Vicentino, Italy.

RANGE. Middle Eocene to Pliocene.

Palaeograpsus bittneri sp. nov. Figs 66, 67

DIAGNOSIS. A *Palaeograpsus* with the lateral margins finely granulated and a larger granule bordering the epigastric lobe; the median part of the dorsal surface is weakly depressed.

NAME. For A. Bittner.

HOLOTYPE. In 61987 (Fig. 66), and paratypes In 61988 (Fig. 67), In 61989–93 from locality S.5538, Upper Miri Formation.

DESCRIPTION. The carapace is subquadrate, almost as broad as long. Short, rounded anterolateral margins lined with several small granules terminate at a weak notch more clearly seen in side view, where a shallow furrow extends back a little before curving to the front. Behind the notch is a larger granule followed by two or three smaller ones; the marginal edge then becomes rounded posteriorly. Long, shallow depressions for the 5th coxae lead by broadly rounded angles to the posterior margin, which is concave and about as wide as the front. The slightly produced front occupies half of the orbitofrontal margin and is almost straight on either side of a

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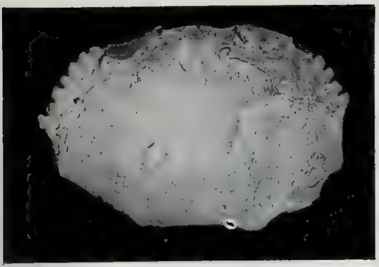
Figs 46, 47 *Portunus woodwardi* sp. nov. From S.5548, Lower Miri Formation, × 2. Fig. 46, **holotype** (♂) In 61923. a, b, dorsal and ventral views. Fig. 47, paratype (♂) In 61924. a, b, dorsal and ventral views showing bopyriform swelling on the left branchial chamber.

Figs 48–53 *Podophthalmus fusiformis* sp. nov. from S.5550, Lower Miri Formation. Fig. 48, **holotype** In 62066, × 2. a, b, dorsal and anterior views. Fig. 49, dorsal view of paratype In 62067, × 3. Fig. 50, ventral view of paratype In 62068, × 3. Fig. 51, dorsal view of paratype In 62070, × 3. Fig. 52, dorsal view of paratype In 62071, × 3. Fig. 53, dorsal view of paratype In 62069, × 3.

Figs 54, 55 *Galene stipata* sp. nov. Fig. 54, **holotype** In 59014 from S.4965, Lower Miri Formation, × 1. a–d, dorsal, ventral, left lateral and anterior views. Fig. 55, anteroventral view to show right cheliped of paratype In 61958 from S.5548, Lower Miri Formation, × 2.

Figs 56a, b *Prepaeduma decapoda* gen. et sp. nov. **Holotype** In 61994 from S.5549, Lower Miri Formation, × 3. a, b, dorsal and ventral views. See also Figs 56c, d (p. 27).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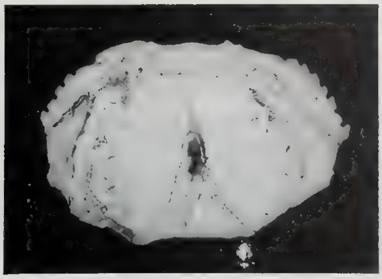
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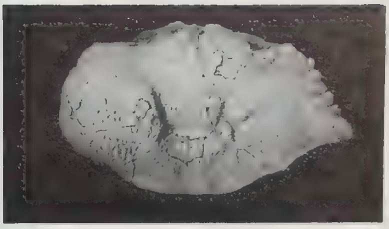
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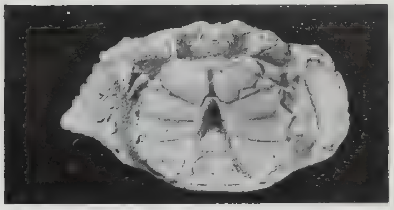
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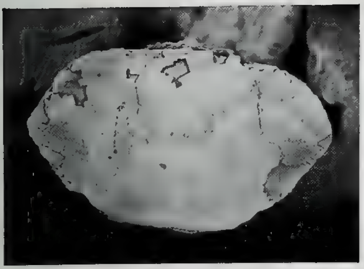
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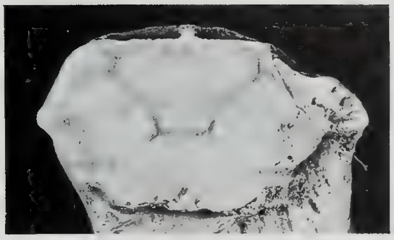
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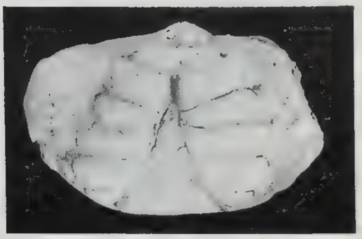
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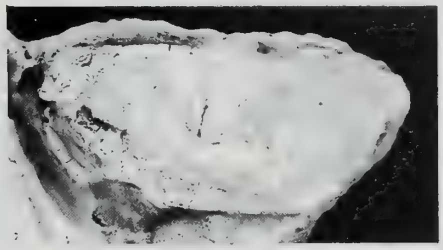
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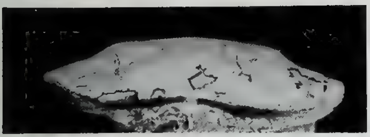
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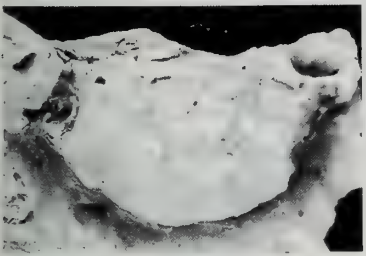
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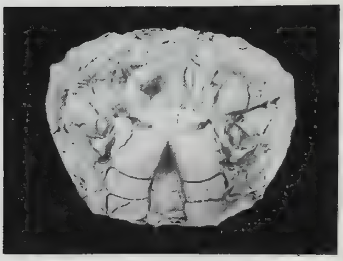
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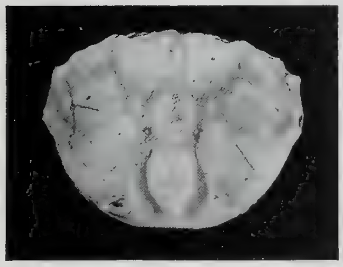
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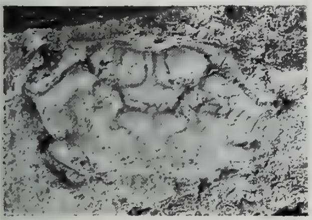
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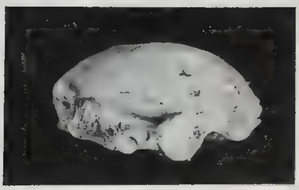
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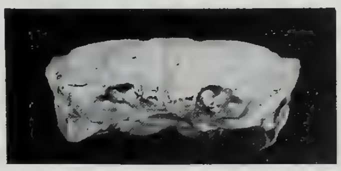
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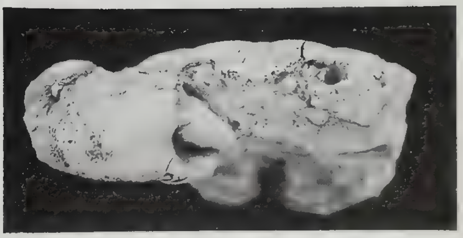
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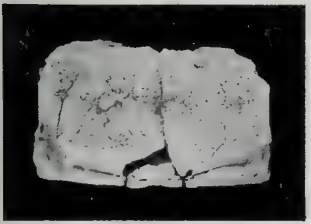
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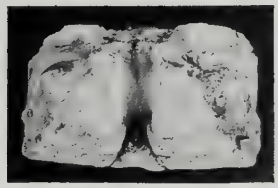

56b

slight median notch, emphasised above by weak epigastric lobes and bordered by a fine ridge continuing round the upper orbital margin. The upper orbital margin is weakly sinuous and terminates in an inconspicuous spine.

The postcervical furrow is strongest where it crosses the midline in a gentle curve; weakening at the outer angles of the mesogastric lobe, it extends forwards and outwards and becomes obsolete before reaching the margin. Very short epimeral adductor muscle scars separate the urocardiac from the branchiocardiac regions. Only the anterior process of the mesogastric lobe is clearly defined and internal moulds show a granule at the lower inner angle of the protogastric lobes. A depression across the base of the mesogastric and basal portions of the protogastric lobes appears deepened posteriorly by tumid mesobranchial lobes and a rounded ridge on the broadly pentagonal, fused cardiac region. Wide, deep furrows extend from the broadest part of the cardiac region parallel with the coxigeal incisions; anterior to these furrows, a shallower branchiocardiac furrow crosses the carapace margin and curves toward the front.

The chelipeds are of much the same length, although the left is the heavier; the manus equals about half the carapace width. The perieopods are long and slender; the merus of the 4th is similar in size to that of the 2nd and 3rd and a little longer than the 5th.

The telson of the male abdomen reaches as far as the 3rd/4th sternite border; the 4th sternites are triangular and the even-sized 5th/8th are chordate in outline.

Discussion. There is a remarkable similarity in the form of *Palaeograpsus bittneri* sp. nov. to *P. guerini* Via, 1959, from the Lutetian of Italy and Spain, to *P. depressus* Quayle & Collins, 1981 its possible derivative, and *P. bartonensis* Quayle & Collins, 1981, the last two from the Upper Eocene of the Hampshire Basin. In *P. bittneri*, however, the cervical furrow is reduced dorsally to a marginal notch; the postcervical is confined to the median part of the carapace and in these respects it is closer to the British species than to *P. guerini*. The front of *P. bittneri* is straighter and its outer angles sharper than in *P. guerini*, but probably not so far advanced as the similarly-shaped front of *P. depressus*.

Superfamily **PINNOTHEROIDEA** de Haan, 1833

Family **PINNOTHERIDAE** de Haan, 1833

Subfamily **PINNOTHERINAE** de Haan, 1833

Genus ***PINNIXA*** White, 1846

Type species. By original designation *Pinnotheres cylindricum* Say, 1818 [ICZN Opinion 85]; from Recent of Jekyll Island, Georgia, U.S.A.

Range. Oligocene to Recent.

Pinnixa aequipunctata sp. nov. Figs 58–61

Diagnosis. A *Pinnixa* with gastro-hepatic furrows more prominent than those dividing the branchial regions. There is a pit on either side of the midline and between them the cervical furrow is shallow: the dorsal surface of the branchial region is evenly pitted.

Name. Referring to the pitted branchial regions.

Holotype. In 61983 (Figs 58a, b), and paratypes In 61984 (Fig. 59), In 61985 (Fig. 60), In 61986 (Fig. 61). All from locality S.5539, Upper Miri Formation.

Description. Carapace with length a little more than half the breadth, moderately rounded longitudinally and nearly flat in transverse section. The antero- and posterolateral margins are well rounded, but leave the lateral margins shortly subparallel. The margin edges are acute and thinly beaded. Ovate orbits, occupying the outer thirds of the orbitofrontal margin, are slightly indented medially by a projection of the upper orbital margin and a short length of the ocular peduncle, seen on the type, is contracted coincidentally. The front is not well preserved. The furrow separating the hepatic from the gastric regions commences immediately behind the outer orbital angle, and is deeper than its posterior extension which partly divides the branchial region. The cervical furrow crosses the midline in a broad curve and is shallower between small pits on either side of the midline. The protogastric lobes are feebly separated anteriorly and only a very shallow furrow separates the confluent, almost circular urogastric and cardiac lobes from the branchial regions. Pits of even size crowd the branchial regions.

Discussion. So far, only a few fossil species of *Pinnixa* have been described; the earliest known, *P. eocenica* Rathbun, 1926 may be distinguished from *P. aequipunctata* in having a more rounded carapace outline, stronger branchial furrows and a narrower cardiac region. Rathbun (1932) described two Miocene species from California: of these *Pinnixa galliheri* differs from the Borneo species in having arcuate rather than straight lateral margins, while *P. montereyensis* is known by only one specimen showing its ventral surface. In the same paper Rathbun describes *Parapinnixa miocenica* (regarded by Via Boada, 1969, as *Pinnixa*) which also has angular lateral angles.

Pinnixa omega sp. nov. Fig. 62

Diagnosis. Carapace with deep grooves separating the mesogastric region from the protogastric region and the protogastric region from the hepatic lobes.

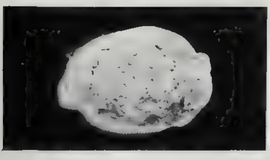
Figs 56c, d, 57 *Prepaeduma decapoda* gen. et sp. nov. Fig. 56c, d, **holotype** In 61994 from S.5549, Lower Miri Formation, × 3. c, d, left lateral and posteroventral views. See also Figs 56a, b (p. 25). Fig. 57, ventral view of paratype In 61996 from S.5550, Lower Miri Formation, × 3.

Figs 58–61 *Pinnixa aequipunctata* sp. nov. Fig. 58, **holotype** In 61983 from S.5539, Upper Miri Formation, × 3. a, b, dorsal and left lateral views of internal mould. Fig. 59, paratype In 61984 from S.5539, Upper Miri Formation, × 3. a, b, dorsal and anterior views of internal mould. Fig. 60, right oblique anterior view to show cheliped, paratype In 61985 from S.5539, Upper Miri Formation, × 5. Fig. 61, manus of right cheliped, paratype In 61986 from S.5539, Upper Miri Formation, × 10.

Fig. 62 *Pinnixa omega* sp. nov. **Holotype** In 61982 from S.5539, Upper Miri Formation, × 3. a, b, dorsal and anterior views.

Figs 63–65 *Xenophthalmus subitus* sp. nov. from S.5539, Upper Miri Formation, × 3. Fig. 63, **holotype** (♀) In 62097. a, b, dorsal and ventral views. Fig. 64, ventral view of abdomen, paratype (♂) In 62098. Fig. 65, ventral view of abdomen, paratype (♂) In 62099.

Figs 66, 67 *Palaeograpsus bittneri* sp. nov. from S.5538, Upper Miri Formation, × 3. Fig. 66, **holotype** In 61987, latex cast of external mould of dorsal. Fig. 67, paratype In 61988, latex cast of external mould of ventral.



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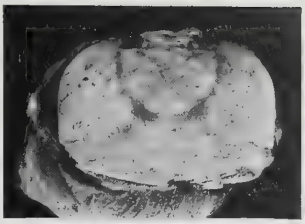
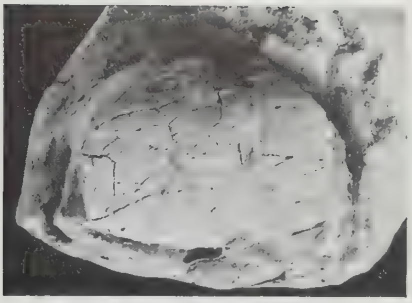
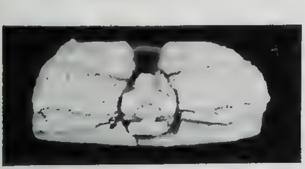


58a



59a



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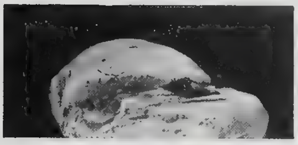
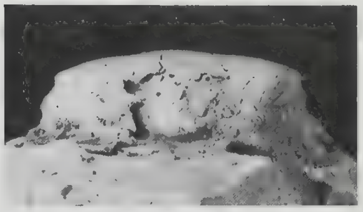


58b



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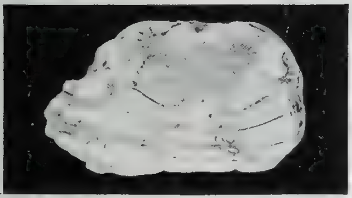

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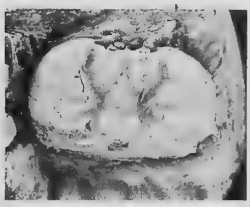

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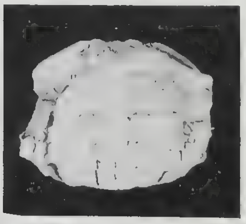
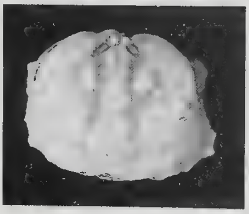
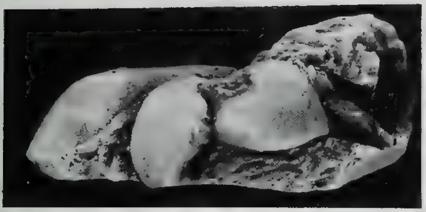


63b



63a



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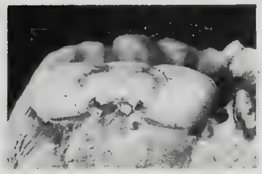
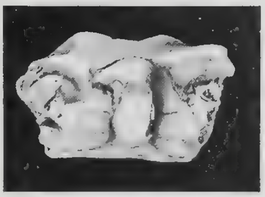


62b



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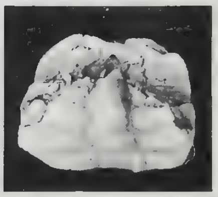
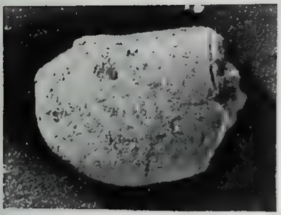


65



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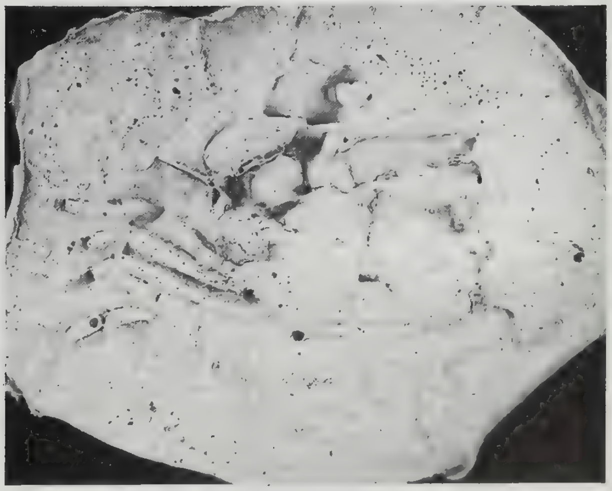

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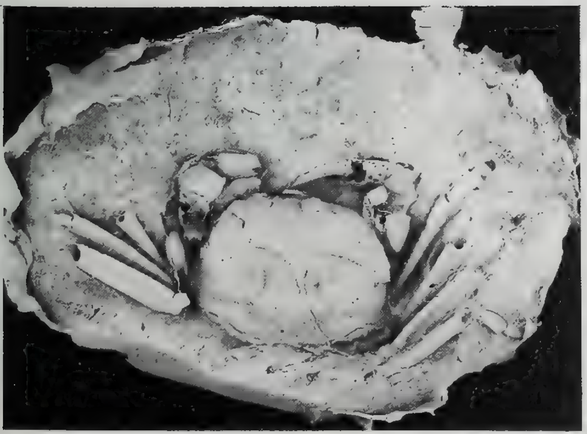


66

NAME. From the resemblance of the hepatic and gastric furrows to the Greek character.

HOLOTYPE. In 61982 (Figs 62a, b) from locality S.5539, Upper Miri Formation.

DESCRIPTION. The transversely subovate carapace is one-third broader than long, and nearly flat in both transverse and longitudinal sections. Small ovate orbits take up the outer fourths of the orbitofrontal margin, which occupies about a third of the carapace width. The upper orbital margin is slightly raised and the front (which is not well preserved) is emphasized above by minute frontal lobes set close to the tip of the anterior mesogastric process. The posterolateral margins are somewhat less rounded than the anterolateral margins, the posterior angle is acute and the wide posterior margin is weakly concave at its outer thirds and (possibly) convex medially; it is bounded by a fine rim. From wide, shallow marginal notches the cervical furrow extends broadly backwards and inwards. Becoming narrower, it curves sharply round the base of the hepatic region to unite with the gastro-hepatic and proto-mesogastric furrows before crossing the midline in a shallow curve; laterally it encloses a small tumid, triangular subhepatic region. From immediately behind the outer orbital angle the prominent gastro-hepatic furrow runs back for half its length, before turning angularly inwards; the proto-mesogastric furrow is only a little less wide. The hepatic regions are weakly tumid bordering the furrow, and the finely tapering anterior process of the isosceles-shaped mesogastric lobe extends to the front. The confluent urocardiac region is lingulate in outline.

DISCUSSION. The deeply incised gastric furrows and their characteristic outline immediately distinguishes *P. omega* from *P. aequipunctata* sp. nov., p. 26, and from all other species of *Pinnixa*. *Pinnixa* species are commonly commensal with annelid worms, living in their burrows and also in the burrows of worm-like holothurians.

Superfamily **HEXAPODOIDEA** Miers, 1886

Family **HEXAPODIDAE** Miers, 1886

Subfamily **HEXAPODINAE** Miers, 1886

Genus ***PREPAEDUMA*** nov.

TYPE SPECIES. *Prepaeduma decapoda* gen. et sp. nov. from the Pliocene of Borneo.

RANGE. Pliocene, Lower to Upper Miri Formation.

DIAGNOSIS. Hexapodid with fifth pair of pereiopods and eighth sternites fully exposed subdorsally. Female abdominal somites unfused; in the male the fourth and fifth abdominal somites are fused.

NAME. Precursor of *Paeduma*. Neuter.

DISCUSSION. Only one genus of hexapodid crab, *Paeduma* Rathbun, 1897 (= *Amorphopus* Bell, 1859 *non* Audinet-Serville, 1839) can be compared with *Prepaeduma*, because it is the only hexapodid genus bearing a fifth pereiopod, although Bell (1859) mentions in describing *Amorphopus cylindraceus* that the fifth pair of pereiopods were reduced to a mere rudiment. Bell further commented that on de Haan's figure he could detect a tubercle at the base of the fourth pereiopod which is probably a vestigial representative of the fifth pereiopod. Manning & Holthuis (1981: 174) transferred *Thaumastoplax orientalis* Rathbun, 1909, *T. chuensis* Rathbun, 1909, and an undescribed species from Japan identified by earlier workers as *T. orientalis*, from *Thaumastoplax* to *Paeduma*. Manning & Holthuis showed that all these species had the third with the fourth, and the fifth with the sixth, male abdominal segments fused, and that in all the abdomen extended forward to the posterior margin of the buccal cavity. *Thaumastoplax* is distinguished from *Paeduma* by having the third to fifth male abdominal segments fused, and the second ambulatory legs are by far the longest and strongest of the walking legs. We are unable to confirm the last character in *P. decapoda,* below, because unfortunately the legs are not preserved. *Thaumastoplax* and *Paeduma* are similar in lacking the oblique striae on the pterygostomian regions common in hexapodid genera.

As noted by Guinot (1979: 114) hexapodid crabs are generally commensal, living in the tubes of annelids and the cavities of hydrozoans. The body has become transversally elongated for ease of entry to these cavities, presumably associated with sideways walking. Guinot (1979: 115) noted that *Paeduma* seemed to conform to the twelfth [*recte*, eleventh] rule of Lankester (1904: 538–9), in which a tendency to atrophy will be seen generally in the front or rear of the tagma. In *Prepaeduma* we probably have an ancestral form in which all the segments and legs are present but in the male only abdominal somites four and five are fused.

Prepaeduma decapoda gen. et sp. nov. Figs 56, 57

DIAGNOSIS. As genus.

NAME. 'Ten-legged'.

HOLOTYPE. In 61994 (♂, Figs 56a–d), from Pliocene, Lower Miri Formation of locality S.5549. Paratypes In 61996 (♂, Fig. 57), In 61997–99 (11 specimens) from Pliocene, Lower Miri Formation of S.5550; paratypes In 62062–5 (6 specimens) from Pliocene, Upper Miri Formation of S.5539.

DESCRIPTION. Carapace length about three-quarters of the breadth; longitudinally very convex, particularly anteriorly, and nearly flat in transverse section. The anterolateral margins are narrowly rounded and the straight posterolateral margins lead by acute posterior angles into wide incisions abutting the 7th sternites. The posterior margin is straight and about as wide as the orbitofrontal margin which takes up about two-thirds of the carapace width. The front is not well preserved; it is rounded with the longitudinal curvature of the carapace and probably did not extend beyond the outer orbital spine. Anteriorly the margin edges are acute and finely ridged; the sides are inclined more or less at right angles to the dorsal surface and the subhepatic region is slightly tumid.

The regions are poorly defined and the cervical furrow is represented by little more than lines running towards the midline from a shallow pit at the head of short, moderately deep epimeral muscle scars. The broad, subtriangular cardiac region is clearly delineated from the branchial regions. Fine granules crowd the dorsal surface.

In the male the abdominal trough is rather narrow between the 6th sternites and broadens about midlength of the 5th pair. The 5th sternites are large, subtriangular with a broadly rounded basal angle and oblique basal edge; the median edge of the 6th pair protrudes slightly beyond the 5th and its basal edge is almost straight in contrast to the indented forward edge. The 7th pair is subrectangular in outline and is the longest.

In the female a fine suture with two pits separates the 4th sternites from the 5th pair which are trapezoidal, and their rounded basal angles protrude beyond the 6th. As in the male the 7th sternites are longest and all are inclined to the midline. The subovate female abdomen is broadest across the 3rd somite and the tip of the rather large subtriangular telson, rounded apically, extends the length of the 5th sternites. Only the small rectangular 3rd and 4th/5th somites of the male abdomen are preserved; the broken anterior margin of the '5th' is about half of the broadest part of the quadrate '4th'.

The male specimen (In 61996, Fig. 57) clearly shows the 5th pereiopod and 8th sternite, both of which are situated subdorsally. An 'appareil d'accrochage du type bouton-pression' (Guinot 1979: 120) is certainly present in the male, represented by a pit in the vertical wall of the abdominal trough on the 4th sternite situated just in front of the 4th/5th sternite boundary.

Discussion. *P. decapoda* is most similar to *Paeduma orientale* (Rathbun, 1909) but differs in the segments of the male abdomen. It is also comparable to *Hexapinus latipes* (de Haan, 1835), which has the third male abdominal segment fused to the fourth and fifth segments.

Subfamily **XENOPHTHALMINAE** Alcock, 1900

Genus ***XENOPHTHALMUS*** White, 1846

Type species. By monotypy *Xenophthalmus pinnotheroides* White, 1846, from the Recent of the Philippines.

Range. Pliocene to Recent.

Xenophthalmus subitus sp. nov. Figs 63–65

Diagnosis. Hepatic regions project anteriorly beyond the frontal region. Front with longitudinal groove which continues between the epigastric lobes. Discontinuous transverse ridge crosses the carapace at the level of the cardiac region.

Name. 'Sudden' or 'unexpected'.

Holotype. In 62097 (Figs 63a, b) and paratypes In 62098 (Fig. 64), In 62099 (Fig. 65), In 62100–19 from locality S.5539, Upper Miri Formation.

Description. The carapace is subovate, about one-fourth broader than long; moderately curved longitudinally, but downturned rather more steeply in front and nearly flat in transverse section. Short anterolateral margins are rounded continuously into the front and thinly ridged; the ridge is a little more accentuated at the outer orbital angles, but becomes obsolete behind the orbits. Anteriorly the sides are inclined at about right angles with a low ridge just above the pleural suture; they become rounded and splayed out posteriorly. Broad, rounded posterior angles lead by shallow incisions for the fifth coxae into a narrow posterior margin which is rather more steeply concave in the male. The very small orbits are obliquely ovate, in line with the longitudinal curvature of the carapace. The front is not produced, sulcate above with small terminal nodes followed by tumid, somewhat elongated epigastric lobes. A transverse, sinuous row of tubercles is formed by one median on the mesogastric lobe, two on each protogastric and one on each epibranchial lobe; behind these, smaller granules on the mesobranchial and one on either side of the median mesogastric form a second, almost parallel row. Another granule occurs just above the coxigeal incision. Curving across the metabranchial lobes a sharp ridge is interrrupted by grooves delimiting the broadly pentagonal cardiac region and continues across its broadest part.

The broadly ovate female abdomen covers the entire ventral surface. The 6th somite is fractionally larger than the 3rd–5th somites, and at the junction of each somite there is a pit in the trough on either side of the raised median portion; on the 3rd somite is a low transverse ridge. The male abdomen is about a third the width of that of the female and parallel-sided.

Discussion. The backward direction of the orbit suggests this species should be assigned to *Xenophthalmus*, but other characters on the carapace, especially the discontinuous transverse ridge level with the cardiac region, invites comparison with *Neoxenophthalmus obscurus* (Henderson, 1893) in which the ridge separates a punctate area from the smooth posterior region. The holotype (In 62097) has the peduncles of the eyes deformed, giving a misleading impression that the orbits are inclined at an oblique angle to the midline (Fig. 63a). The Brunei species has all the regions more strongly expressed than in *Xenophthalmus pinnotheroides* White, 1846, and lacks the ridge from the posterior margin crossing the metabranchial and joining the cardiac transverse ridge.

This group of hexapodids is probably commensal with annelids in relatively shallow water in the 5–30m range and on a muddy bottom.

Superfamily **OCYPODOIDEA** Rafinesque, 1815

Family **OCYPODIDAE** Rafinesque, 1815

Subfamily **MACROPHTHALMINAE** Dana, 1852

Genus ***MACROPHTHALMUS*** Latreille, *in* Desmarest 1823

Type species. By subsequent designation of H. Milne Edwards, May, 1841: *Gonoplax transversus* Latreille, 1817; from Recent of the Indian Ocean.

Range. Miocene to Recent.

Subgenus ***MAREOTIS*** Barnes, 1967

Type species. By original designation *Macrophthalmus japonicus* de Haan, 1835; from Recent of the Indo-Pacific region.

Range. Pliocene to Recent.

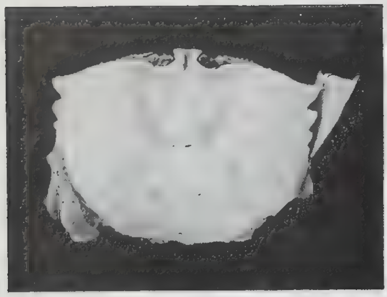
Macrophthalmus (Mareotis) wilfordi sp. nov. Figs 68–72

1961 *Macrophthalmus latreilli* (Desmarest): Wilford: 102; pl. 39.

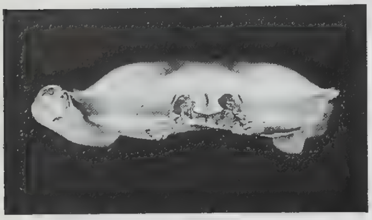
Diagnosis. The carapace is widest between the tips of the outer orbital spines; without transverse lines of granules on the dorsal surface; the fixed finger of the cheliped is depressed.

Name. For G.E. Wilford.

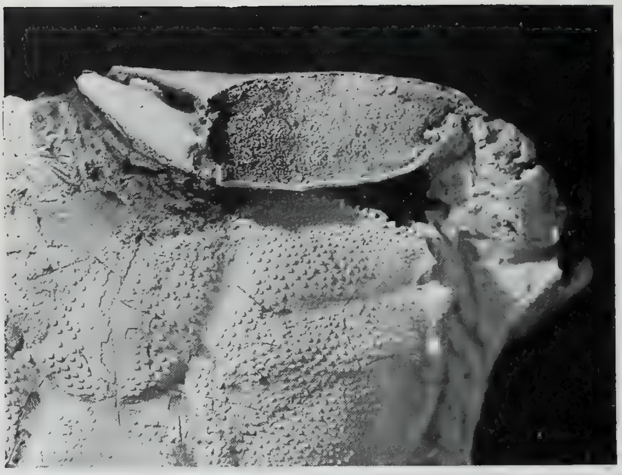
Holotype. In 59000 (Figs 68a, b). Paratypes In 59001–4,



68a



68b



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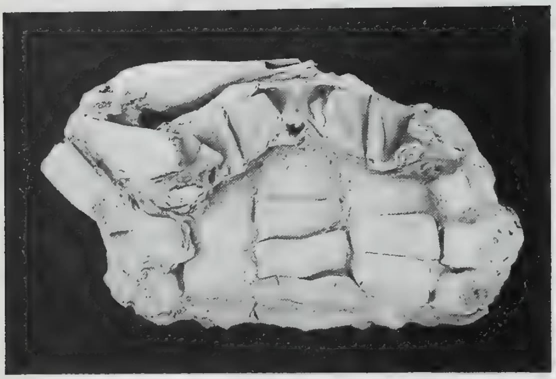

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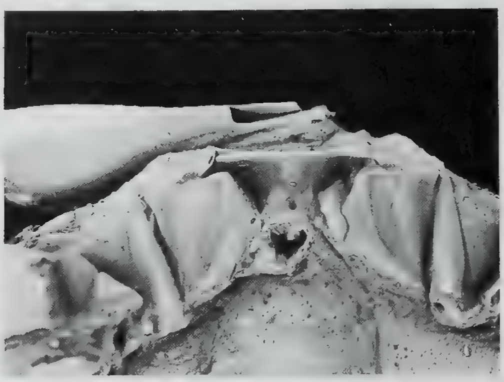

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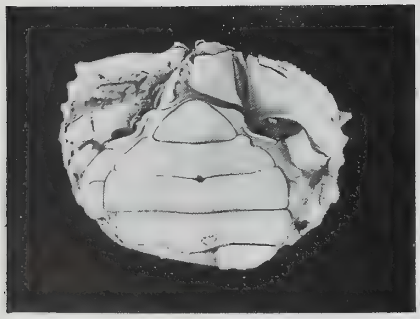

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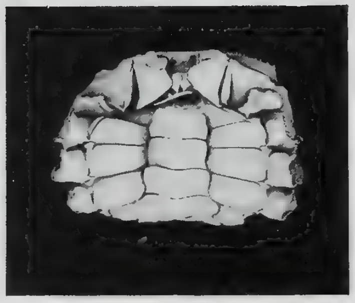

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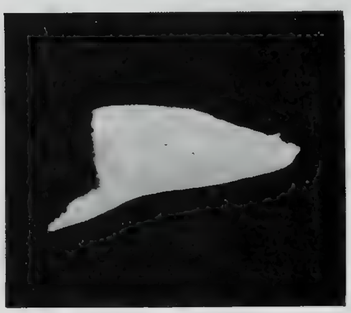

72

Figs 68–72 *Macrophthalmus (Mareotis) wilfordi* sp. nov. from S.4918, ?late Middle Pleistocene. Fig. 68, **holotype** In 59000, × 1. a, b, dorsal and anterior views. Fig. 69, paratype In 62120. a, anterolateral angle and incomplete cheliped, × 3. b, ventral view, × 1.5. c, epistome, × 3. Fig. 70, ventral view of abdomen, paratype (♀) In 59005, × 1.5. Fig. 71, ventral view of abdomen, paratype (♂) In 59008, × 1. Fig. 72, propodus, paratype In 61810, × 1.

Table 2 Stratigraphical distribution of fossil crab species from the Neogene of Borneo.

	Lower Miocene	Middle Miocene	Upper Miocene	Lower Miri Fm	Upper Miri Fm	Seria Fm	Middle Pleistocene
Raninoides sp.	–	–	–	–	×	–	–
Dorippe frascone (Herbst) *tuberculata* subsp. nov.	–	–	–	×	–	–	–
Calappa sexaspinosa sp. nov.	–	–	–	×	–	–	–
Podophthalmus fusiformis sp. nov.	–	–	–	×	–	–	–
Charybdis feriata (Linn.) *bruneiensis* subsp. nov.	–	–	–	–	–	–	×
Portunus obvallatus sp. nov.	–	–	–	×	×	–	–
Portunus woodwardi sp. nov.	–	–	–	×	×	–	–
Galene stipata sp. nov.	–	–	–	×	×	×	–
Parthenope (Rhinolambrus) sublitoralis sp. nov.	–	–	–	×	–	–	–
Ampliura simplex gen. et sp. nov.	–	–	–	–	–	×	–
Drachiella guinotae sp. nov.	–	–	–	×	–	–	–
Iphiculus granulatus sp. nov.	–	–	–	–	–	×	–
Iphiculus miriensis sp. nov.	–	–	–	×	×	–	–
Iphiculus sexspinosus sp. nov.	–	–	–	–	×	×	–
Leucosia longiangulata sp. nov.	–	–	–	×	–	–	–
Leucosia serenei sp. nov.	–	–	–	×	×	–	–
Leucosia tutongensis sp. nov.	–	–	–	×	×	–	–
Myra brevisulcata sp. nov.	–	–	–	×	–	–	–
Myra subcarinata sp. nov.	–	–	–	×	×	–	–
Myra trispinosa sp. nov.	–	–	–	×	×	–	–
Nucia borneoensis sp. nov.	–	–	–	×	–	–	–
Nucia calculoides sp. nov.	–	–	–	×	–	–	–
Nucia coxi sp. nov.	×	–	–	–	–	–	–
Nucilobus symmetricus gen. et sp. nov.	–	–	–	×	–	–	–
Pariphiculus gselli Beets *beetsi* subsp. nov.	–	–	–	×	–	–	–
Pariphiculus papillosus sp. nov.	–	–	–	×	–	–	–
Pariphiculus verrucosus sp. nov.	–	–	–	×	–	–	–
Philyra granulosa sp. nov.	–	–	–	×	×	–	–
Typilobus marginatus sp. nov.	–	×	–	–	–	–	–
Typilobus sp.	×	–	–	–	–	–	–
Palaeograpsus bittneri sp. nov.	–	–	–	–	×	–	–
Pinnixa aequipunctata sp. nov.	–	–	–	–	×	–	–
Pinnixa omega sp. nov.	–	–	–	–	×	–	–
Prepaeduma decapoda gen. et sp. nov.	–	–	–	×	×	–	–
Xenophthalmus subitus sp. nov.	–	–	–	–	×	–	–
Macrophthalmus (Mareotis) wilfordi sp. nov.	–	–	–	–	–	–	×

In 59005 (Fig. 70), In 59006–7, In 59008 (Fig. 71), In 59009–11 (about 50 specimens), In 61810 (Fig. 72), In 62120 (Figs 69a–c). All from locality S.4918, ? late Middle Pleistocene.

DESCRIPTION. The carapace is subquadrate in outline, widest between the tips of the outer orbital spines and with the regions distinctly defined by furrows. The moderately bilobed front is narrow, deflexed and constricted between the bases of the ocular peduncles; the front edge is smooth but the sides are finely granulate; there is a deep, narrow median furrow and a few surface granules. The upper orbital border is curved and slopes slightly backwards; the margin is lined with small, rounded granules; the lower orbital margin is studded along its entire length with longer, tubercular granules. The outer orbital spine is large, rectangular with granulated margins; it is directed outwards and slightly forwards and is separated from the 2nd lateral spine by a broad U-shaped notch. The 2nd lateral spine is somewhat weaker than the former and does not project beyond it, its anterior margin is convex and both that and the posterior one are weakly granulate; a shallow notch separates it from the small, triangular 3rd lateral spine.

With the exception of a narrow frontal strip and a few small central areas the dorsal surface is covered with coarse granules. On each metabranchial region two longitudinal rows of granules extend subparallel to the lateral margin; the inner row is 'broken' and becomes sigmoidal centrally. The lateral margins are subparallel and lined with granules.

The sides of the 4th and 5th somites of the male abdomen are nearly straight and parallel, while the sides of the 6th are slightly convex and taper a little distally.

The chelipeds associated with the carapaces are incomplete, and of those attributed to *M. wilfordi* none has a ridge on the outer margin of the palm, the upper part of the outer margin is granulate especially proximally, and the lower margin is smooth. The fixed finger is deflexed and one left-hand example has a large crenulated tooth proximally on the cutting edge, and the lower margin is granulate with the granules decreasing in size distally.

DISCUSSION. In having a narrow front with a well-developed ocular constriction, longitudinal granulate rows on the metabranchial lobes, a deflexed finger and, in the male, an abdomen with sides almost parallel, it would appear that the new species has already diverged considerably from the hypothetical ancestral form as envisaged by Barnes (1967: 250).

Macrophthalmus wilfordi has all the general characters essential to the subgenus *Mareotis* which one can reasonably expect to find preserved among fossil specimens. The occurrence of the greatest carapace width across the tips of the outer orbital spines instead of the 2nd anterolateral spines (common to the extant species of *Mareotis*) cannot be considered sufficient grounds to exclude it from that subgenus.

Of the nine Recent species placed by Barnes (1967, 1970) in *Mareotis, M. japonicus* de Haan compares favourably with and could well be descended from *M. wilfordi*. Apart from the position of the greatest carapace width, the former species may be distinguished by the upper and lower orbital margins being studded with similar-sized granules, by the absence of granules lining the frontal margin, and the presence of a transverse row of granules on the metabranchial lobes. According to Barnes (1967: 226) the inner longitudinal row of granules on the metabranchial lobes on Japanese forms of the Recent species is 'broken', as in *M. wilfordi*, while in Australian and North Chinese forms (Barnes 1970; 228) it is entire.

A superficial resemblance exists between *M. wilfordi* and *M. (Euplax) latreillei* (Desmarest, 1817), but the latter may be distinguished by the straight orbitofrontal margin, transverse rows of granules on the metabranchial lobes and a straight, undeflexed fixed finger.

Note. Barnes (1966), in revising the genus *Euplax* H. Milne Edwards, 1852 (type species *E. leptophthalmus* Milne Edwards, 1852, by subsequent designation of Barnes, 1966: 370) noted that *E. leptophthalmus* belonged to *Macrophthalmus* of the *M. latreillei* group. Later, Barnes (1967) erected a series of subgenera for the genus *Macrophthalmus*, including *M. (Venitus)* with type species by original designation *M. latreillei* (Desmarest, 1817). Thus it can be seen that *Euplax* is in fact a senior subjective synonym of *Venitus*. Further *Cyphoplax* Haime, 1855 (type species *Goneplax impressa* Desmarest, 1817 by monotypy, = *M. latreillei* (Barnes 1977: 280)) is also a senior subjective synonym of *Venitus*, but a junior subjective synonym of *Euplax*.

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Two new pseudosciurids (Rodentia, Mammalia) from the English Late Eocene, and their implications for phylogeny and speciation

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SYNOPSIS. Assemblages formerly referred to *Treposciurus intermedius* and *Suevosciurus palustris*, from the Solent Group (Late Eocene) of Hordle and of localities in the Isle of Wight (Hampshire Basin), are shown to differ markedly from the type specimens of these species. They are here described as two new species belonging to the original genera. The differences between these two superficially similar species are clarified and evidence for phylogeny and speciation events within the genera is discussed.

INTRODUCTION

Bosma (1974), when describing the rodent faunas of the Isle of Wight Late Eocene and Early Oligocene, attributed two small pseudosciurid species to *Treposciurus intermedius* (Schlosser 1884) and *Suevosciurus palustris* (Misonne 1957). The lectotype of the former is a dentary from the Phosphorites du Quercy of Escamps (old locality), Tarn, southern France, of imprecise but probable Late Eocene age. The holotype of the latter is an upper M^1 or M^2 from the Sables de Boutersem (Early Oligocene – i.e. immediately post-Grande Coupure) of Hoogbutsel, Belgium. Both type specimens are thus geographically, and in at least one case also stratigraphically, distant from the southern English referred material. They also differ from them in both size and morphology. The *Treposciurus* is rare, but new material from the Hordle Mammal Bed makes it better known.

Abbreviations

The following relate to institutes and/or their specimen numbers. BSPG = Bayerische Staatssammlung für Paläontologie und historische Geologie, München; GIU = Instituut voor Aardwetenschappen, Rijksuniversitet Utrecht; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles; M = register numbers of the Mammal Section, Department of Palaeontology, Natural History Museum, London.

Synonymies

Procedure and terminology follow Matthews (1973).

SYSTEMATIC DESCRIPTIONS

Order **RODENTIA**
Superfamily **THERIDOMYOIDEA**
Family **PSEUDOSCIURIDAE**

Genus ***TREPOSCIURUS*** Schmidt-Kittler 1970

TYPE SPECIES. *Treposciurus mutabilis* Schmidt-Kittler 1970; Late Eocene, Bavaria, southern Germany.

Treposciurus gardneri sp. nov. Figs 1–14

?vp 1973 *Suevosciurus* (*Microsuevosciurus*) aff. *minimus* (Major 1873); Hartenberger: 16; pl. 1, figs 7–9, 11–13.
vp. 1974 *Treposciurus intermedius* (Schlosser 1884); Bosma: 49–52; pl. 6, figs 3–10.
vp. 1974 *Suevosciurus palustris* (Misonne 1957); Bosma: pl. 5, fig. 7.
v. *1980* *Treposciurus intermedius* (Schlosser 1884); Hooker & Insole: 39.
v. *1982* *Treposciurus intermedius* (Schlosser 1884); Russell *et al.*: 57.
v. 1986 *Treposciurus intermedius* (Schlosser 1884); Hooker: 308–311.
v. *1987* *Treposciurus intermedius* (Schlosser 1884); Collinson & Hooker: 292.
v. *1987* *Treposciurus* sp. nov.; Hooker: 112.
v. 1989 *Treposciurus* sp. nov.; Hooker: fig. 2.

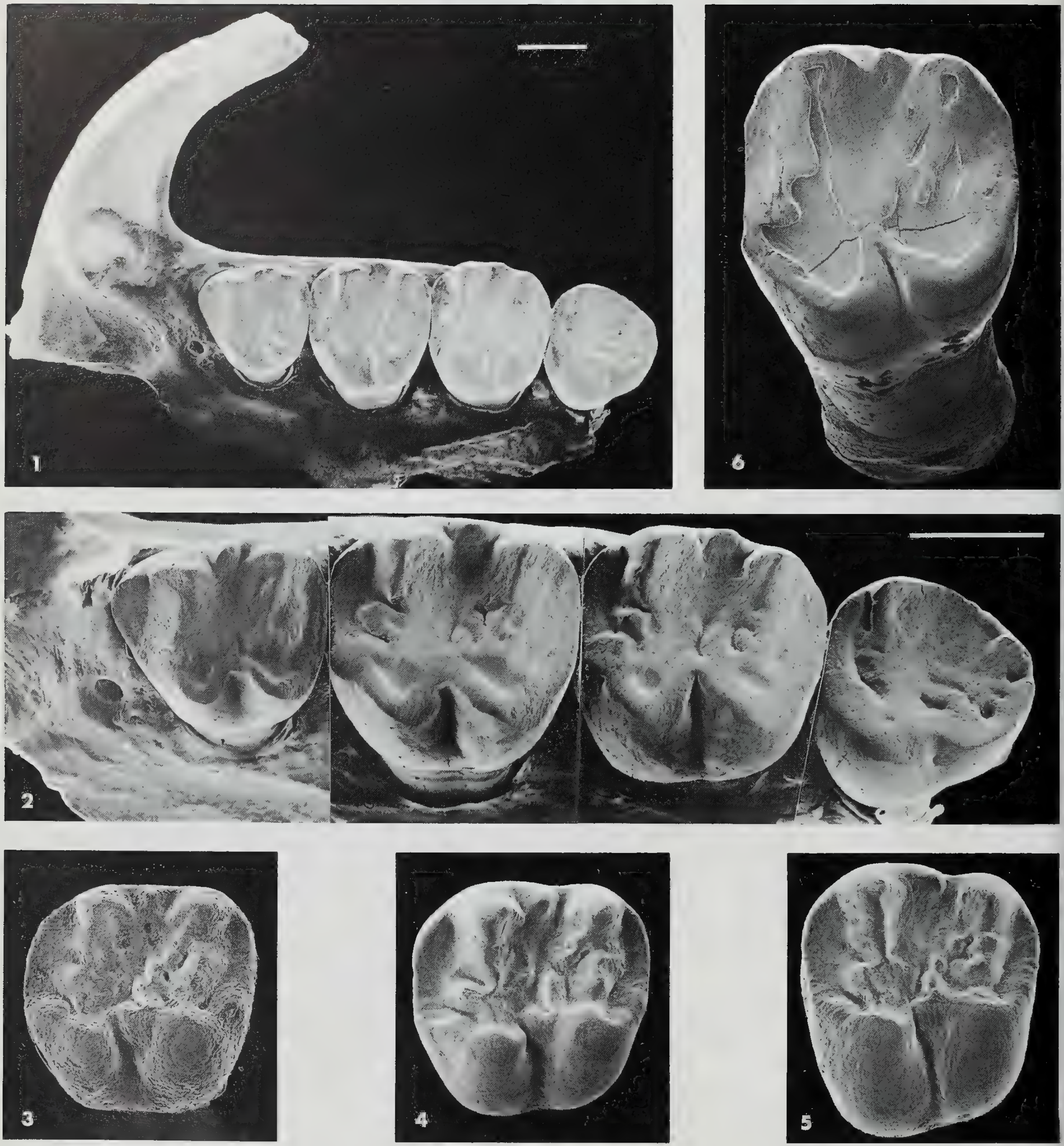
HOLOTYPE. Right maxilla with DP^4, M^{1-3} (M44472).

PARATYPES. DP^4 (M44473), 7 $M^{1/2}$ (M44474–80), 3 DP_4 (M44481–3), 2 P_4 (M44484–5), right dentary fragment with worn M_{1-2} (M44486), 9 $M_{1/2}$ (M44487–95), 4 M_3 (M44496–9).

NAME. After Mr R.G. Gardner who collected the type series.

TYPE HORIZON AND LOCALITY. Mammal Bed (see Cray 1973), Totland Bay Member, Headon Hill Formation (see Insole & Daley 1985; previously informally referred to as Lower Headon Beds), Hordle, Hampshire.

REFERRED MATERIAL. Isolated teeth described and figured by Bosma (1974) from sample localities HH1 and HH2, Totland Bay Member; HH3 and other sample localities from 'below the main lignite band', Hatherwood Limestone Member – two M^3s and an $M_{1/2}$ from HH3 (GIU 492, 412 and 499) and an $M^{1/2}$ and an $M_{1/2}$ from HH4 (GIU 480 and 426), referred by Bosma to *Suevosciurus palustris* also belong here; all Headon Hill Formation, Headon Hill, Isle of Wight. Also from sample locality WB2A, Bembridge Marls Member, Bouldnor Formation, Whitecliff Bay, Isle of Wight. An $M^{1/2}$ (M51083) from a dark clay at top of limestone overlying *Cyrena cycladiformis* bed (Bristow *et al.* 1889), Totland Bay Member; a DP^4 (M51084) from shelly lenses at base of lignite bed, Hatherwood Limestone Member (including



Figs 1–6 Scanning electron micrographs (SEMs) of maxilla and upper cheek teeth in occlusal view of *Treposciurus gardneri* sp. nov., Solent Group, late Eocene. Figs 1–5, Mammal Bed, Totland Bay Member, Headon Hill Formation, Hordle, Hants. Figs 1–2, **holotype**, right maxilla, with DP^4, M$^{1-3}$ and part of zygomatic arch (reversed) (M44472); 2 shows details of the teeth. Figs 3–5, paratype right M$^{1/2}$s (reversed) (M44474–6). Fig. 6, Bembridge Limestone Formation, Headon Hill, Isle of Wight. Referred right M$^{1/2}$ (reversed) (M51085). Scale bars = 1 mm; specimens uncoated.

sample locality of HH3); isolated upper and lower M1/2s (M44500, M51085–7, M51104) from argillaceous beds within the Bembridge Limestone Formation (including HH6–7 of Bosma, 1974); all Headon Hill; and an M_3 from above a calcareous sandstone, Bembridge Marls Member (level of WB2 of Bosma, 1974), Whitecliff Bay. Probably also the isolated cheek teeth described and figured by Hartenberger (1973) from the upper Calcaire de Fons, Fons 4, Gard, France, as *Suevosciurus* (*Microsuevosciurus*) aff. *minimus*.

DIAGNOSIS. Small species of *Treposciurus* (mean length of $M^{1/2}$ 1·77 mm); cheek teeth with relatively shallow basins, without dense enamel wrinkling or reticulation; upper preultimate molars and DP^4 with dentine cored (visible only after heavy wear – Fig. 6), interrupted metalophule I, usually extending buccally to the metacone and joining the endoloph between the hypocone and sinus; lower cheek teeth with weak mesoconid protruding only a short distance into sinusid; lower molars with medium-sized anteroconid, joined to interrupted metalophulid by anterolophulid; $M_{1\text{-}2}$ mesial hypoconid wall more or less vertical, encroaching little on sinusid, which consequently has open appearance; buccal corners of upper molars often noticeably rounded, reflecting lingual retreat of anteroloph and posteroloph.

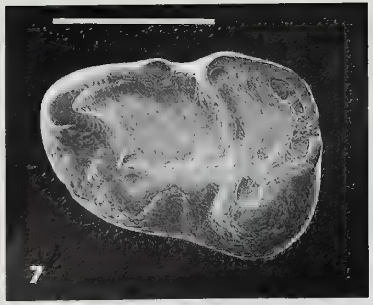
DIFFERENTIAL DIAGNOSIS. Other *Treposciurus* species are larger, tend to have densely wrinkled enamel and/or a lesser development of $M^{1\text{-}2}$ metalophule I and have lower molars with stronger mesoconids and weaker anteroconids (see Schmidt-Kittler 1971; Bosma 1974; Hooker 1986).

DESCRIPTION. P_4, DP_4 and $M_{1/2}$ tooth types are made known for the first time and contribute significantly to an understanding of the species and its distinction from *T. intermedius* (see p. 39). Variation in the separation of the protoconid and metaconid on the two P_4s can be seen in Figs 11–12. Complex variation in development of $M^{1\text{-}2}$ metalophule I and of the coarse enamel folds in upper and lower molars can be seen in Figs 1–14 and Bosma (1974: pl. 6, figs 3–10). Other features such as strength of the lower cheek tooth mesoconid and anteroconid are remarkably constant, within the relatively small sample. The rounding of the buccal corners of upper molars is striking when present, but by no means constant. It is most marked in the specimens from WB2A (Bosma 1974: pl. 6, figs 6, 8–10). The outline shape of M_3 varies much (Figs 10, 14) in a similar way to that documented for *Treposciurus helveticus preecei* from the Bartonian of Creechbarrow (Hooker 1986: pl. 17, figs 4, 6), and reflects differing development of the entoconid and transverseness versus obliquity of the mesial margin. The length measurements of upper and lower preultimate molars have a low coefficient of variation (see Table 1). The holotype maxilla is broken a short distance anteriorly and medially of DP^4 so the extent of the incisive foramen is unknown.

Other assemblages differ from the type assemblage slightly in size, but not in morphology (Table 1). The teeth from Fons 4 have mean lengths of $M^{1/2}$ (1·62 mm) and $M_{1/2}$ (1·65 mm) (Hartenberger 1973:16) slightly less than has the type assemblage of *T. gardneri*, with little overlap of measurements. Morphology clearly shows the Fons 4 assemblage is very

Table 1 Statistics of length and width measurements of cheek teeth of *Treposciurus*. (N = number of specimens; OR = observed range; x̄ = mean; s = standard deviation; v = coefficient of variation. Measurement in brackets is estimate). * = measurements taken from epoxy casts.

		Length					Width				
Sp./loc.	Tooth	N	OR	x̄	s	v	N	OR	x̄	s	v
T. gardneri	DP^4	2	1·68–1·88	1·78			2	1·52–1·68	1·60		
Hordle	$M^{1/2}$	8	1·66–1·80	1·77	0·048	2·70	8	1·61–2·04	1·82	0·143	7·85
Mammal Bed	M^3	1		1·60			1		1·76		
	DP_4	3	1·72–1·98	1·82			3	1·24–1·38	1·29		
	P_4	2	1·76–1·80	1·78			2	1·44–1·54	1·49		
	$M_{1/2}$	10	1·76–1·96	1·88	0·065	3·42	10	1·50–1·72	1·63	0·066	4·09
	M_3	4	1·86–2·02	1·94			3	1·52–1·66	1·58		
T. gardneri above Cyrena cycladiformis Bed	$M^{1/2}$	1		1·90			1		(1·96)		
T. gardneri	DP^4	1		1·92			1		1·66		
HH3–4	*$M^{1/2}$	1		1·65			1		1·64		
	*M^3	2	1·56–1·67	1·62			2	1·53–1·64	1·59		
	*$M_{1/2}$	2	1·74–1·86	1·80			2	1·45–1·56	1·51		
T. gardneri	$M^{1/2}$	1		2·10			1		2·38		
Bembridge Limestone	$M_{1/2}$	1		2·14			1		1·84		
*Lectotype	DP_4	1		2·48			1		1·80		
T. intermedius	M_1	1		2·56			1		2·24		
Quercy	M_2	1		2·72			1		2·26		
	M_3	1		2·60			1		1·92		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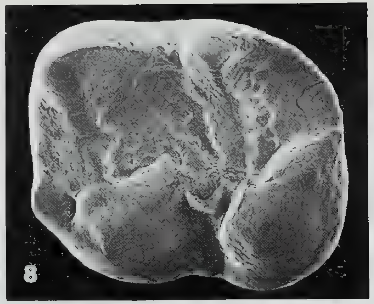
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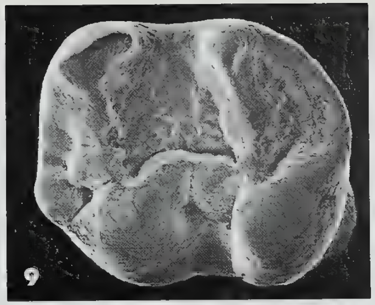
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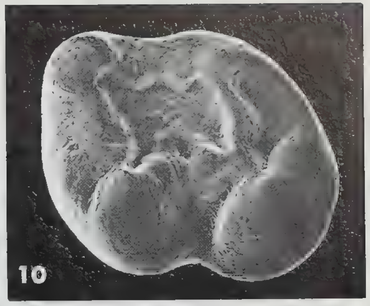
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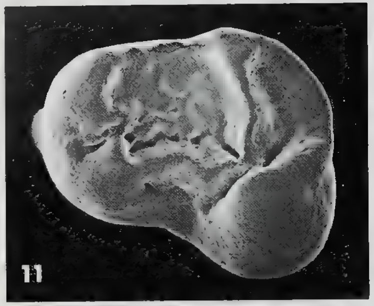
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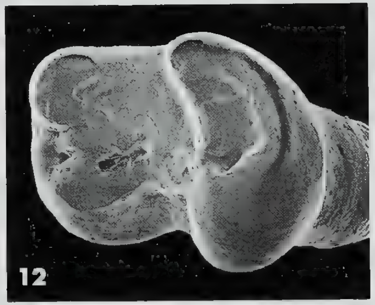
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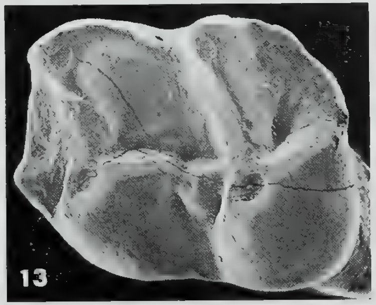
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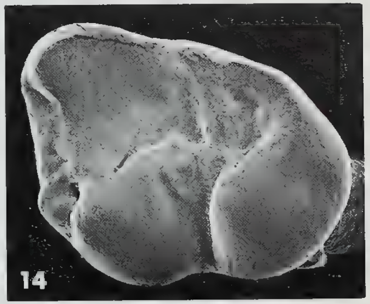
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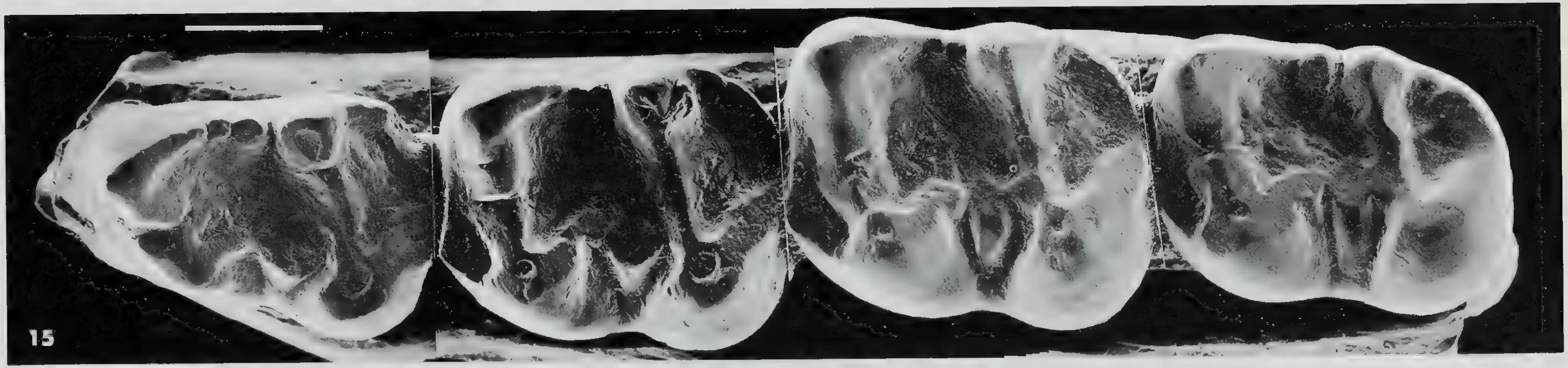
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Figs 7–15 SEMs of lower cheek teeth in occlusal view of *Treposciurus*, late Eocene. Figs 7–12, 14, paratypes of *Treposciurus gardneri* sp. nov., from the Mammal Bed, Hordle, Hants. Fig. 7, right DP_4 (reversed) (M44481); Fig. 8, right $M_{1/2}$ (reversed) (M44487); Fig. 9, left $M_{1/2}$ (M44488); Fig. 10, left M_3 (M44496); Figs 11–12, left P_4s (M44484–5); Fig. 14, right M_3 (reversed) (M44497). Fig. 13, left $M_{1/2}$ of *T. gardneri* sp. nov. from the Bembridge Limestone Formation, Headon Hill, Isle of Wight (M51104). Fig. 15, epoxy cast (coated with gold-palladium) of right DP_4, $M_{1\text{-}3}$ of lectotype of *T. intermedius*, from the Phosphorites du Quercy, France (original BSPG.1879XV-192). Scale bars = 1 mm; original specimens uncoated.

closely related and, as Bosma (1974:53) noted, not a *Suevosciurus*, but the distinct plots of measurements leave doubt over precise conspecificity. The $M^{1/2}$s from WB2A described by Bosma also lie outside the measurements of the type assemblage, being slightly larger. The small number of specimens (3) suggests that there would be overlap if more were known, but the single $M^{1/2}$ from the Bembridge Limestone is also slightly larger than any from the type assemblage. The Bembridge Limestone Formation and the Bembridge Marls Member of the Bouldnor Formation are demonstrably younger than the Mammal Bed at Hordle, by superposition, and Fons 4 is considered older, e.g. according to the evolutionary grade of its *Choeropotamus* (see Sudre 1978). It would therefore seem that there is a trend towards size increase, which could indicate that the Fons 4, Hordle and WB2 assemblages are segments of a single lineage. Curiously, however, the two upper molars from HH1 recorded by Bosma (1974) are also larger than any in the type assemblage. As the Mammal Bed and HH1 (only 8·5 km apart) both contain *Thalerimys headonensis*, they are penecontemporaneous (belonging to Bosma's '*Isoptychus*' *headonensis* Zone). Either none of the assemblages has yet been adequately sampled to show the size range, or a more complex pattern of size than a simple increase through time may pertain.

Discussion

Explanation of reidentification.
The type series of '*Sciuroides*' *intermedius* Schlosser, 1884 consisted of two dentaries and a maxilla from the old Quercy Phosphorites locality of Escamps, southern France. Dehm (1937) selected one of the dentaries as lectotype. Schmidt-Kittler (1970) erected the genus *Treposciurus* for *T. mutabilis* Schmidt-Kittler 1970 (type species) and for '*Sciuroides*' *intermedius* Schlosser 1884. Schmidt-Kittler (1971) removed the maxilla of the type series of *T. intermedius* from that species, because the posterior border of its incisive foramen reached back to P^4 in Schlosser's figure, thus contrasting with another Quercy maxilla figured by Thaler (1966), the dental match of which was better. Bosma (1974) claimed that the posterior border of the incisive foramen was damaged in the paralectotype maxilla and that the specimen could still belong in *T. intermedius*. Bosma was relying on referred maxillary specimens from Quercy for comparison with her Isle of Wight material, as her knowledge of the lower dentition was restricted to a single M_3. She noted that these upper molars and the rather undiagnostic M_3 were morphologically similar to those of *T. intermedius*, but that they were slightly smaller. Whatever the true identity of the paralectotype maxilla, the lectotype dentary is all that one can rely upon for potential identification of other *T. intermedius* specimens. Inaccuracy of old Quercy locality names makes it impossible to recognize any unequivocal topotypes. Nevertheless, several upper dentitions from old Quercy collections appear to match adequately the lowers of the lectotype and other specimens; their distinguishing features have been tabulated by Schmidt-Kittler (1971: tab. 4). They include upper molars which differ strikingly from *T. gardneri* in having a symmetrical endoloph, coarsely wrinkled enamel and no metalophule I.

It can be seen that the teeth of the lectotype of *T. intermedius* are significantly larger than the equivalents in *T. gardneri* (Figs 7–15). They have a stronger mesoconid and a higher length/width ratio. The M_{1-2} hypoconid encroaches further mesially on the sinusid and DP_4 and M_3 each have a prominent mesostylid. The last feature is variable in *T. gardneri*, occurring in one out of three DP_4s and incipiently in one out of ten $M_{1/2}$s; the others are constant for the available specimens.

What makes *T. gardneri* a *Treposciurus* and not a *Suevosciurus*? The recognition that the tooth types previously regarded as P_4^4 are in reality DP_4^4 (Hooker 1986) removes one distinction previously maintained. The most recently emended diagnoses of *Treposciurus* and *Suevosciurus* (Hooker 1986: 308, 315) do not polarize the characters, but a restriction to those in the advanced state is shown in Fig. 16. In *Suevosciurus*, upper and lower cheek teeth have basins that are deeper and more concave, the antero- and posterolophs and lophids tend to be more prominent and the transverse lophs are more distinct; the upper molars tend to have an uninterrupted, more symmetrical endoloph, with any expression of metaconule 2 or metalophule I (which lack a dentine core) restricted to a lingual section; metalophule II joins the hypocone; M^3 shows more distal reduction with, in the contemporaneous species from Hordle, total absence of metalophule II, a much shallower sinus and more mesially positioned protocone (compare the present figures with Bosma 1974: pl. 6, fig. 10). The lower molars usually lack an anterolophulid and have a stronger mesoconid which, in the contemporaneous species from Hordle (amongst others), is usually linked by a crest to the mesiobuccal corner of the hypoconid (Figs 22–23); and DP^4 usually has a concave mesiolingual margin (Figs 17–18).

Evidence for a late Eocene speciation event.
Hooker (1986) formulated a model of cladogenetic speciation in the genus *Treposciurus*. He envisaged a morphologically very variable *T. helveticus* of the Bartonian giving rise around the Bartonian–Ludian boundary to *T. intermedius* and *T. mutabilis* by respective selection of two morphs present together in the ancestral species and by size differentiation. He divided *T. helveticus* (raised to species level from *T. mutabilis helveticus* Schmidt-Kittler 1971) into two subspecies: a nominate one from Eclépens B, Switzerland, and *T. h. preecei* from Creechbarrow. Current detailed study of the Eclépens B material (Hooker & Weidmann, in prep.) shows that *T. h. helveticus* involves greater complexity. The Eclépens B *Treposciurus* is therefore simply referred to as *Treposciurus helveticus* Schmidt-Kittler 1971, and the subspecies *T. helveticus preecei* Hooker 1986 is hereby raised to species level as *Treposciurus preecei* Hooker 1986 *new rank*.

These nomenclatural changes do not affect the evidence for the speciation event, but they do mean that the ancestral species is now *T. preecei*, and one daughter species is *T. gardneri*, whilst the other daughter branch is at present an unresolved complex comprising *T. mutabilis*, *T. helveticus* and *T. intermedius*. The evidence based on character analysis is presented in Fig. 16. Here a cladogram shows the splitting of *Treposciurus gardneri* from the rest and also the characters linking the genus *Treposciurus* to its nearest sister taxon *Suevosciurus*. Character polarity was obtained by outgroup comparison with the rest of the Pseudosciuridae.

1B. DP^4, M$^{1-2}$ with constant, incomplete, dentine-cored metalophule I, usually extending buccally to metacone; and no dense enamel wrinkling.

2. Upper molar buccal corners often strongly rounded.
3. Lower molar mesoconid reduced.
4. Lower molar hypoconid scarcely overhanging sinusid.
5. Lower molars usually with anterolophulid (N.B. also present in advanced assemblages of *T. mutabilis*).
6. Mean M$^{1/2}$ length less than 2·1 mm.
7B. M$^{1-2}$ commonly with dense enamel wrinkling and rarely with metalophule I.

8. Lower molar anteroconid small or absent.

1A. M$^{1-2}$ with incomplete, dentine-cored metalophule I and no dense enamel wrinkling in some individuals.
7A. M$^{1-2}$ with dense enamel wrinkling and no metalophule I in some individuals.

9. Upper molar endoloph usually broken in early wear stages.

10. Upper molar mesocone frequently present.
11. Tendency for upper molar endoloph to fold mesiobuccally into a small sinus.

12. Complete protolophule I and metalophule II on M$^{1-2}$; complete metalophulid on lower molars and DP$_4$.
13. M$^{1-2}$ metaconule 2 reduced.
14. M$^{1-2}$ with non-dentine-cored, lingually restricted metalophule I.

15. DP^4 with concave mesiolingual margin.

16. Upper cheek teeth with postparacristae and premetacristae curved lingually.

17. Upper cheek teeth with relatively large mesostyle.
18. Enamel wrinkling on P$^4_4$ and M$^3_3$.
19. DP^4 usually with bicuspid parastyle.
20. Lower molars with incipient antesinusid.
21. P^4 parastyle relatively prominent.

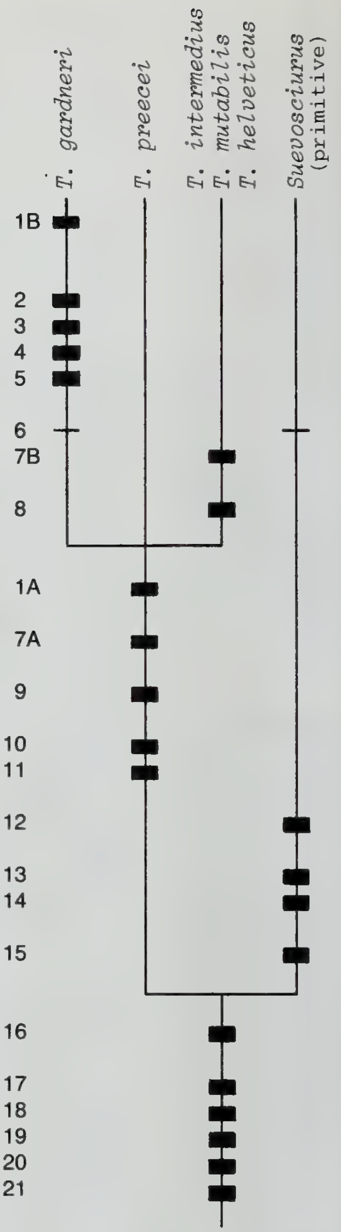


Fig. 16 Cladogram of species of *Treposciurus* and the genus *Suevosciurus*. Synapomorphies indicated by broad bar, parallelisms by narrow bar. Characters 1 and 7 are multistate.

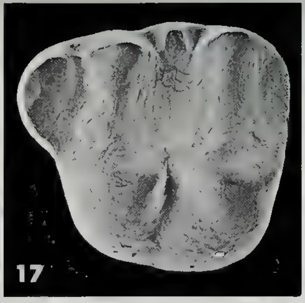
Genus *SUEVOSCIURUS* Dehm 1937

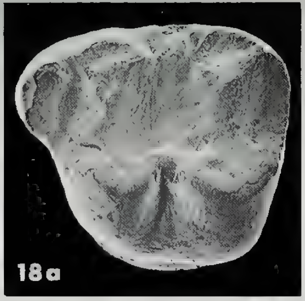
TYPE SPECIES. *Sciuroides fraasi* Major 1873.

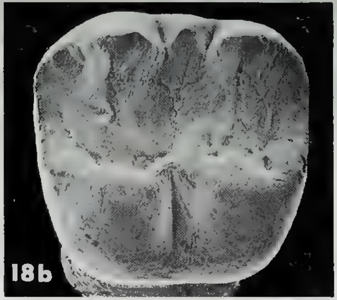
Suevosciurus bosmae sp. nov. Figs 17–23, 30E, F

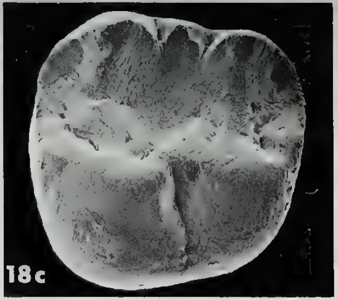
vp. 1974 *Suevosciurus palustris* (Misonne 1957); Bosma: 34–44; pl. 5, figs 7–9.
v. *1980* *Suevosciurus palustris* (Misonne 1957); Hooker & Insole: 39.
vp. *1982* *Suevosciurus palustris* (Misonne 1957); Russell *et al.*: 57.
v. 1986 *Suevosciurus*; Hooker: 322–327.
v. *1987* *Suevosciurus* sp. 1; Collinson & Hooker: 292.
v. *1987* *Suevosciurus* sp. nov.; Hooker: 112.
v. *1989* *Suevosciurus* sp. nov.; Hooker: fig. 2.

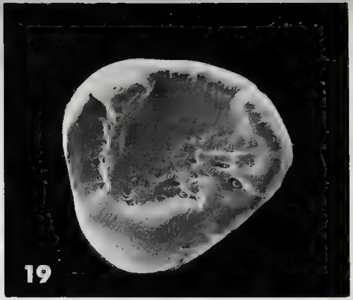
HOLOTYPE. Right DP^4–M^2 (M51095) (Fig. 18). This specimen is chosen because it shows associated cheek teeth of one individual. Although found isolated, they were from the same sample and their matching interstitial facets demonstrate association. A left DP^4 of identical morphology, size and wear state to the holotype DP^4 is probably also associated (Fig. 17), but as a conservative approach it is listed as a paratype.

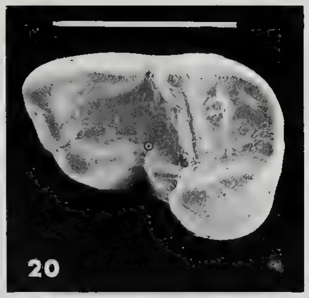


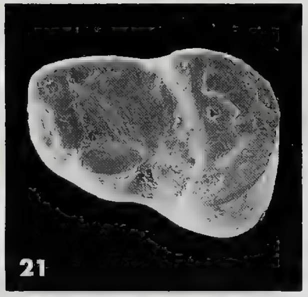


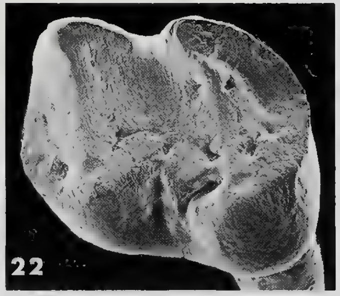


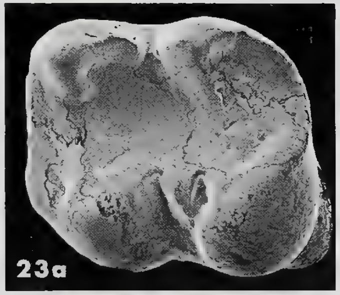


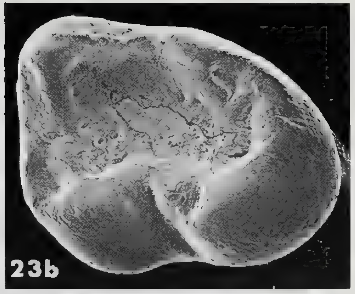


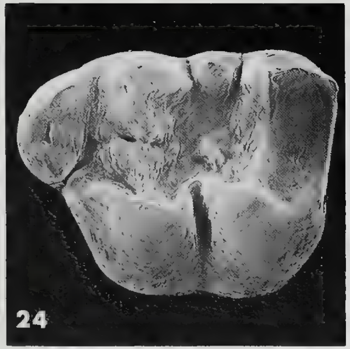


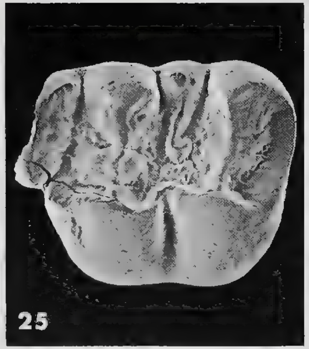


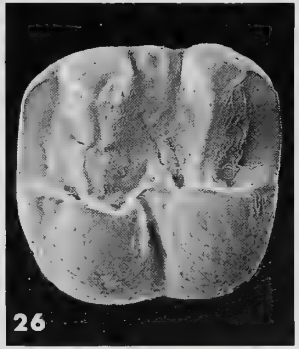


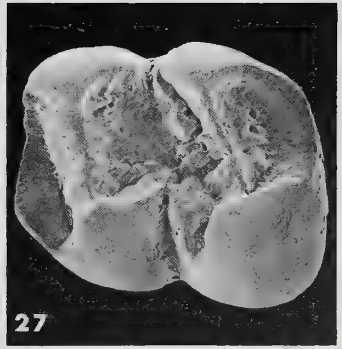


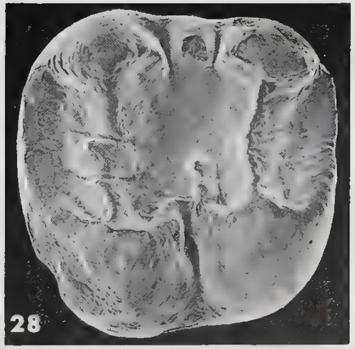












Figs 17–28 SEMs of cheek teeth in occlusal view of *Suevosciurus*, Solent Group, late Eocene, Isle of Wight. Figs 17–23, *S. bosmae* sp. nov., from green clay below How Ledge Limestone, Headon Hill. Fig. 18, **holotype**, associated right DP^4 (a), M^1 (b), M^2 (c) (reversed) (M51095). Figs 17, 19–23 are paratypes: Fig. 17, left DP^4 (M51096); Fig. 19, epoxy cast of left M^3 (original GIU.941); Fig. 20, epoxy cast of right DP_4 (reversed) (original GIU.816); Fig. 21, epoxy cast of left DP_4 (original GIU.815); Fig. 22, left $M_{1/2}$ (M51098); Fig. 23, associated right M_2 (A) and M_3 (B) (reversed) (M51097). Figs 24–27, *S. fraasi*, from the Bembridge Limestone Formation, Headon Hill. Figs 24–25, left DP^4s (M51090–1; the latter's parastyle is slightly broken); Fig. 26, left $M^{1/2}$ (M51093); Fig. 27, left $M_{1/2}$ (M51094). Fig. 28, left $M^{1/2}$ (M49489) of *S. ehingensis*, from the Bembridge Limestone Formation, Headon Hill. Scale bar = 1 mm; casts are coated with gold or gold palladium, originals are uncoated.

PARATYPES. Left DP^4 (M51096) (Fig. 17); left M^3 (GIU941) (Fig. 19); right DP_4 (GIU816) (Fig. 20); left DP_4 (GIU815) (Fig. 21); left $M_{1/2}$ (M51098) (Fig. 22); right $M_{2\text{-}3}$ (M51097) (Fig. 23).

NAME. For Dr Anneke Bosma, Utrecht, in recognition of her work on fossil rodents.

TYPE HORIZON AND LOCALITY. Green clay below the How Ledge Limestone (includes Bosma's (1974) sample locality HH2) near top of Totland Bay Member, Headon Hill Formation, SW Headon Hill, Isle of Wight.

REFERRED MATERIAL. Topotype isolated teeth M33371, M51096 and M51098–51102. Also Bosma's (1974) material in the GIU from the Totland Bay Member of Headon Hill (HH1, 2) (topotypes) and Totland Bay; and Lignite Bed in Hatherwood Limestone Member of Headon Hill (HH3, 4, B and C) (except GIU 426, 480, 492 and 499 which belong to *Treposciurus gardneri*). Additional isolated teeth from shelly lenses at base of lignite bed (same level as HH3 of Bosma 1974) (M51106–51129).

DIAGNOSIS. Mean length of $M^{1/2}$ = 1·55 mm; range 1·39–1·67 mm. P^4_4 absent. DP^4 mean length/width ratio 1·17–1·19. M^3 without distinct metalophule II and often with weak paraconule . DP^4 with width at paracone and protocone less than width at metacone and hypocone; no lingual parastylar notch. Lower molars nearly always with crest joining mesoconid to hypoconid.

DESCRIPTION. Much of the morphological variation has been described qualitatively by Bosma (1974). An attempt has been made in Tables 2–3 to quantify this to provide a means of comparison with *Suevosciurus authodon* from the Bartonian of Creechbarrow (Hooker 1986). Dividing lines between categories are admittedly often arbitrary and can often be documented only in relatively little-worn teeth, but despite these shortcomings this methodology can still demonstrate broad trends and differences. Only the assemblages from the green clay below the How Ledge Limestone (including HH2) near the top of the Totland Bay Member, and the shelly lenses at the base of the lignite bed in the Hatherwood Limestone (including HH3) were considered large enough for this quantitative treatment, and neither are as large as that from Creechbarrow.

Table 2 Percentage character analysis of upper cheek teeth of *Suevosciurus bosmae* from the green clay below How Ledge Limestone (HH2) and from shelly lenses at base of Lignite Bed (HH3). 'Scoring units' give states for characters described in the left-hand column. The numbers given under the tooth-headed columns on the right are percentages and refer to the number of teeth showing that particular character state. The final lines of figures in brackets in the left-hand column are the respective numbers of each tooth type represented. See Hooker (1986:296, text-fig. 31) for relevant dental nomenclature diagram.

Characters + (N) of respective teeth	Scoring units	DP^4		M^{1-2}		M^3	
		HH2	HH3	HH2	HH3	HH2	HH3
Metalophule I shape: metaconule 1 only (1), ridge (2) (8) (5) (16) (8)	1	12	0	6	25		
	2	88	100	94	75		
Metalophule I joins endoloph (1), hypocone (2), metalophule II (3), endoloph and hypocone (4), hypocone and metalophule II (5), endoloph and metalophule II (6), all three (7), none (0) (8) (6) (13) (9)	0	12·5	0	7·5	22		
	1	37·5	33·2	62·0	78		
	2	37·5	16·7	23·0	0		
	3	0	16·7	0	0		
	4	0	0	0	0		
	5	0	16·7	0	0		
	6	12·5	16·7	7·5	0		
	7	0	0	0	0		
Metalophule II broken/unbroken (14) (9) (31) (22) (15) (9)	B	14	0	16	36	100	0
	U	86	100	84	64	0	0
Enamel wrinkling (0–3) (13) (9) (23) (16) (11) (10)	0	46	11	0	6	0	0
	1	23	56	56	50	9	10
	2	23	33	35	31	73	80
	3	8	0	9	13	18	10
Mesostyle size (0–4) (16) (9) (37) (23) (16) (11)	0	0	0	0	0	6	27
	1	19	0	16	22	0	0
	2	56	67	70	56	0	18
	3	19	33	14	22	44	9
	4	6	0	0	0	50	46
Mesostyle saliency: prominent (3), slight (2), non- (1), ectoflexus (0) (15) (9) (33) (20) (16) (9)	0	0	22·0	18	20	0	0
	1	20	33·5	70	55	6	33
	2	67	33·5	12	25	69	67
	3	13	11·0	0	0	25	0

Table 2 (contd)

Characters + (N) of respective teeth	Scoring units	DP^4		M^{1-2}		M^3	
		HH2	HH3	HH2	HH3	HH2	HH3
Mesoloph length (0–2) (14) (9) (32) (21) (15) (11)	0	7	0	16	33	100	100
	1	57	89	75	43	0	0
	2	36	11	9	24	0	0
Protolophule I broken/unbroken (11) (8) (35) (19) (8) (9)	B	0	0	6	11	25	89
	U	100	100	94	89	75	11
Metaconule 2 absence/presence (16) (9) (38) (23)	0	50	89	79	78		
	1	50	11	21	22		
Hypolophule absent (0), partial (1), complete (2) (13) (9) (35) (20)	0	85	78	77·0	75		
	1	15	22	11·5	15		
	2	0	0	11·5	10		
Posteroloph broken/unbroken lingually (7) (9) (22) (18)	B	0	11	23	17		
	U	100	89	77	83		
Mesocone absence/presence (15) (9) (38) (21) (16) (11)	0	100	100	100	100	87·5	100
	1	0	0	0	0	12·5	0
Sinus depth: shallow (1) to deep (4) (17) (9) (38) (21) (15) (11)	1	0	0	0	0	60	45·5
	2	12	67	10	5	40	45·5
	3	70	22	82	81	0	0
	4	18	11	8	14	0	9
Protostyle absence/presence (16) (8) (38) (21) (15) (10)	0	75	37·5	89	76	100	90
	1	25	62·5	11	24	0	10
Hypostyle absence/presence (9) (8) (25) (4)	0	78	100	52	50		
	1	22	0	48	50		
Paraconule absent (0), small (1), large (2) (16) (9) (37) (23) (13) (10)	0	0	0	0	0	0	10
	1	6	0	3	13	62	70
	2	94	100	97	87	38	20
Endoloph broken (1), complete (2) (8) (9) (21) (17) (7) (11)	1	0	11	0	12	0	18
	2	100	89	100	88	100	82
DP^4 parastyle bicuspid (9) (8)	0	44	37·5				
	1	56	62·5				
DP^4 mesiolingual margin concave (16) (8)	0	6	37·5				
	1	94	62·5				

Because of the small sample numbers, first and second molars were not distinguished. Many of the characters show a distribution similar to that in *S. authodon*. However, there is a general tendency in a number of the characters for one morphology in the range to dominate more than in *S. authodon*. In other words there is a slight reduction in variation. M^3 shows the greatest number of differences. Its distal reduction compared to *S. authodon* means that most specimens have lost their mesoloph and metalophule II (and, in the few that retain it, it is discontinuous), and reduced the depth of the sinus, the incidence of a protostyle, and the size of the paraconule. Mesiodistal elongation of the mesostyle is restricted to M^3, having been lost from the other upper cheek teeth. In both upper and lower cheek teeth there is an increase in enamel wrinkling intensity on DP_4^4–M_2^2. In the lower molars the hypoconulid present in some $M_{1/2}$s of *S. authodon* is not encountered in the *S. bosmae* assemblages. There is also a reduction in the incidence of the distal crest to the hypolophulid. There is a slight shift in the average position of attachment of the ectolophid to the hypolophulid in M_3, so that in a greater proportion the attachment is at or very close to the hypoconid. The biggest difference is in the increase in the proportion of teeth where the mesoconid is linked to the buccal side of the hypoconid by a crest, thus

Table 3 Percentage character analysis of lower cheek teeth of *Suevosciurus bosmae* from HH2 and HH3, as in Table 2.

Characters + (N) of respective teeth	Scoring units	DP$_4$ HH2	DP$_4$ HH3	M$_{1-2}$ HH2	M$_{1-2}$ HH3	M$_3$ HH2	M$_3$ HH3
Distance along hypolophulid from hypoconid of junction with ectolophid (7) (6) (20) (20) (9) (12)	<¼	71	83	65	80	100	83
	¼	29	0	35	20	0	17
	no link	0	17	0	0	0	0
Anteroconid size (22) (18) (9) (12)	1			27	17	0	33
	2			32	44	89	67
	3			36	39	11	0
	4			5	0	0	0
Anterolophulid absent (0), weak (1) (20) (16) (6) (12)	0			85	62·5	100	42
	1			15	37·5	0	58
Mesoconid with crest linking buccally with hypoconid (10) (6) (24) (21) (9) (12)	0	50	83	21	19	0	0
	1	50	17	79	81	100	100
Enamel wrinkling (0–3) (6) (6) (14) (16) (7) (10)	0	0	0	0	0	0	0
	1	50	100	43	44	29	20
	2	33	0	43	50	71	60
	3	17	0	14	6	0	20
Mesostylid absence/presence (10) (6) (23) (21) (9) (12)	0	100	83	96	81	44	92
	1	0	17	4	19	56	8
Ectostylid absence/presence (10) (6) (24) (21) (9) (12)	0	100	100	100	95	100	100
	1	0	0	0	5	0	0
Hypoconulid absence/presence (8) (6) (16) (17) (6) (11)	0	100	100	100	100	100	100
	1	0	0	0	0	0	0
Distal crest to hypolophulid absence/presence (8) (6) (16) (18) (6) (11)	0	100	100	100	94	100	64
	1	0	0	0	6	0	36

isolating the distal part of the sinusid as a discrete fossa. The change is most marked in M$_3$, least marked in DP$_4$. Linkage makes it impossible to allocate mesoconid length categories (cf. Hooker 1986).

None of the morphological differences between these two assemblages of *S. bosmae* appears significant. A possible exception is the M^3 protolophule I, which shows a dominantly broken or interrupted state in the Hatherwood Limestone (HH3) assemblage, in contrast to both the How Ledge Limestone (HH2) and Creechbarrow assemblages, but in common with those of later *S. fraasi* (Schmidt-Kittler 1971:42).

Discussion

Distinction of *S. bosmae* from other small *Suevosciurus*.
Hooker (1986:327) proposed that 'teeth from the Headon Beds (referred by Bosma 1974 to *S. palustris*)' should be placed in a new species, but did not name it (herein named *S. bosmae*). He explained that the assemblages in question have upper cheek teeth with a constantly larger mesostyle, whereas in all those of true *S. palustris* (admittedly few and restricted to the type assemblage from Hoogbutsel) the mesostyle is either very small or absent. Moreover, the only two known lower molars of *S. palustris* (both IRSNB.IG18061) have a mesoconid that is not joined by a crest to the mesiobuccal corner of the hypoconid. Common occurrence of this state is shared with *S. minimus* (Schmidt-Kittler 1971: 48; pl. 2, fig. 5) and *S. authodon* (Hooker 1986: 321). Most lower cheek teeth of *S. bosmae* have the crest joining mesoconid to hypoconid, in common with assemblages of *S. fraasi* and *S. ehingensis* from southern Germany (Schmidt-Kittler 1971: 42–47). Interestingly, they are also paralleled by some individuals of *Treposciurus m. mutabilis* (Schmidt-Kittler 1971: 53, fig. 22i).

It is relatively simple to distinguish *S. bosmae* from similarly-sized *S. palustris*, but less so from other assemblages of small *Suevosciurus*. Hooker (1986: 325), using mainly published measurements, combined data from the Hampshire Basin and Bavaria (southern Germany) to produce a phylogenetic pattern of change in *Suevosciurus* assemblages through time. It essentially followed the concept of Schmidt-Kittler (1971) of two evolving lineages in the latest Eocene and Oligocene of southern Germany, except that it removed *S.*

minimus from a common ancestral position, replacing it with the taxon here named *S. bosmae*. An unsolved problem over the two lineage model of Schmidt-Kittler was the near total reliance on size for distinguishing each lineage, which itself undergoes size increase with time. On this basis, therefore, one cannot identify certain of the assemblages without recourse to knowledge of their age. Bosma (1974: 41–43) thus resorted to an arbitrary division of species on size, which could be considered more parsimonious in the absence of other morphological evidence. Hooker (1986: 326–327) found a gradual increase in length/width proportions of DP^4, through at least the lower part of the sequence, which served to distinguish further some of the similarly-sized assemblages, although problems remained in the probable region of differentiation of *S. fraasi* and *S. ehingensis*.

One of the assemblages which Schmidt-Kittler (1971) placed in *S. fraasi* and Bosma (1974) placed in *S. palustris* is from Ehrenstein 1. This fissure filling contains faunas of two different ages, labelled A and B, so intermixed that they can only be distinguished by comparing each element with those in stratified deposits of known age (Schmidt-Kittler 1969, 1971). The later fauna (B) dates from just after the Grande Coupure, the earlier (A) from the middle of the late Eocene, approximately the age of the Lacey's Farm Limestone Member, Headon Hill Formation of the Isle of Wight. Schmidt-Kittler (1971) considered that of the three *Suevosciurus* species, *S. minimus*, the most primitive, came from the A fauna, whereas *S. fraasi* and *S. ehingensis* came from the B fauna. This means that from just pre-Grande Coupure time (Bernloch 1A/Weissenberg 2) onwards, the otherwise constantly sized *S. fraasi* lineage underwent a rapid size decrease (Ehrenstein 1B) followed by similar increase soon afterwards (Ehingen 12) (see Hooker 1986: text-fig. 38). Schmidt-Kittler (1971: 47) noted some minor morphological differences between his *S. fraasi* and *S. ehingensis* lineages: slightly blunter and more voluminous main cusps and somewhat weaker parastyle on DP^4 in the latter. In fact there is a tendency for DP^4s of post-Grande Coupure assemblages of *S. fraasi* to be dominated by the two morphs that Schmidt-Kittler (1971: 42) described: lingually displaced parastyle, causing a very oblique buccal parastyle margin (his fig. 16b); and notch in the mesial outline just lingual to the parastyle (his fig. 16d). In *S. ehingensis* these morphs are either rare or less clearly developed. The pre-Grande Coupure assemblages referred to *S. fraasi* are less distinct but in common with the post-Grande Coupure ones tend to have the widths of DP^4 across paracone–protocone and metacone–hypocone approximately equal. In *S. ehingensis* the mesial width tends to be slightly shorter than the distal width, in common with *S. bosmae* and *S. authodon* (Fig. 30). DP^4s referred to *S. fraasi* in the Ehrenstein 1 assemblage are morphologically less distinct than the other post-Grande Coupure assemblages and, together with their small size, would thus fit better in the Ehrenstein 1A than the 1B fauna.

Recently, Heissig (1987) has described a new small species of *Suevosciurus*, *S. dehmi*, from the immediately post-Grande Coupure Bavarian fissure filling of Mohren 31. The type assemblage is slightly larger than *S. bosmae* but overlaps slightly with it. It could weaken the evidence for the timing of the speciation event envisaged here by potentially supporting the B age for Ehrenstein 1 *S. fraasi* (the intermediate-sized species), through the latter's possible identification as *S. dehmi*. It does not, however, disprove it. Heissig (1987:102, fig. 1) did not include the plot of the intermediate-sized *Suevosciurus* from Ehrenstein 1, but, from Schmidt-Kittler's (1971) text-fig. 20, it would superimpose the type assemblage of *S. dehmi*. Unfortunately, Heissig did not diagnose *S. dehmi* on characters other than size and it is thus difficult to fit it into a scheme based on morphology. However, his figure (Heissig 1987: pl. 1) of the holotype right dentary with DP_4 (not P_4), M_2 and M_3 shows the molar mesoconids joining the hypoconids as is usual for *S. fraasi*, *S. ehingensis* and *S. bosmae*. If the intermediate-sized *Suevosciurus* from Ehrenstein 1 is indeed *S. dehmi*, then its relationships appear closer to *S. fraasi* than to *S. ehingensis*, perhaps introducing paraphyly for *S. fraasi*. However, decision must await publication of morphological details of *S. dehmi*.

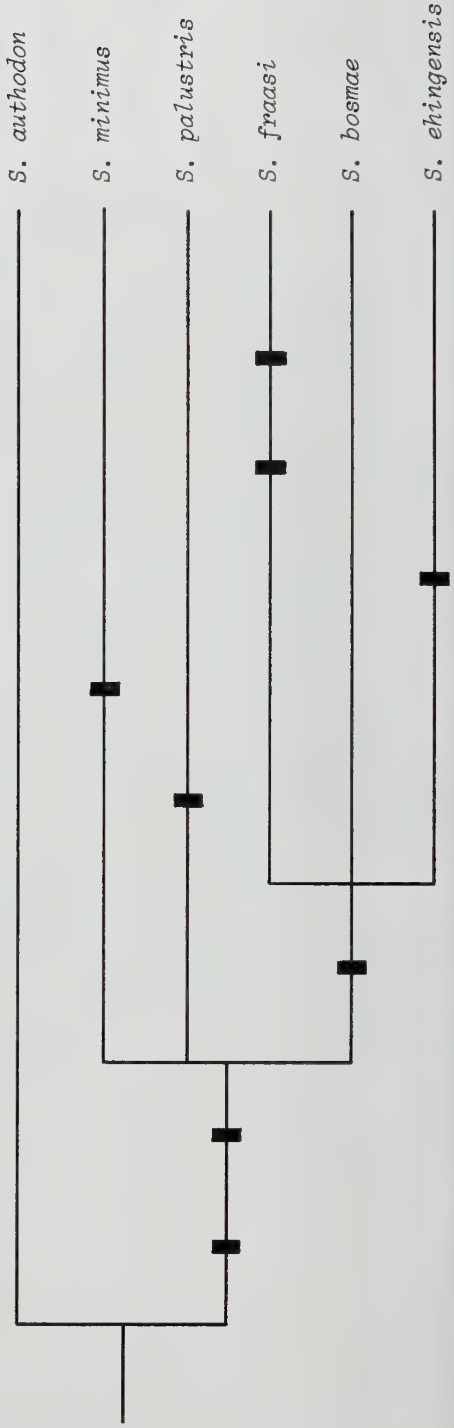
Evidence for a late Eocene speciation event.

To clarify ideas of relationships of the advanced species of *Suevosciurus* (i.e. those that have lost P^4_4), a cladistic analysis is presented here, using the admittedly variable morphological differences in addition to size. *S. authodon* is used as outgroup to polarize the characters. The placement of *S. palustris* is doubtful, as neither DP^4_4 nor P^4_4 tooth types are known, and assumes that characters 7 and 8 are in the advanced state (Fig. 29).

If the Ehrenstein 1 assemblage referred to *S. fraasi* is from the A fauna, as advocated above, it is envisaged that initial differentiation of *S. fraasi* and *S. ehingensis* from the probable ancestral species *S. bosmae* took place, in the former by protocone expansion causing mesial broadening with incipient lingual parastyle notching of DP^4 but with little size increase, and in the latter simply by a greater increase in size unaccompanied by DP^4 shape changes (Figs 30, 31). According to this model the most primitive *S. fraasi* assemblage would be that of Ehrenstein 1, whereas the most primitive *S. ehingensis* assemblage would be that of Lacey's Farm Quarry (Lacey's Farm Limestone Member) (identified on size as *S. fraasi* by Bosma & Insole 1976). There seems also to be a slight size increase of DP^4 over the molars in *S. fraasi*, so that DP^4s from Ehrenstein 1 are about the same size as those from Lacey's Farm Quarry, whereas the molars of the former are smaller; by the time of Weissenburg 8, *S. ehingensis* DP^4s had enlarged proportionally also (Fig. 30). Subsequent patterns of change, in addition to size increase in both lineages (causing advanced assemblages of *S. fraasi* to have character 3), involve repeated elongations and shortenings of DP^4 (Hooker 1986: text-fig. 39), as well as subtle shape changes. None of these, however, affects recognition of the diagnostic *S. fraasi* DP^4s provided assemblages are large enough. These changes thus comprise variation within a lineage which could be discriminated taxonomically at the level of stratigraphical subspecies (e.g. as Franzen, 1968, has done for *Palaeotherium*).

In further support of the speciation model, rare specimens of both *S. fraasi* and *S. ehingensis* have been found in the argillaceous beds of the Bembridge Limestone Formation of Headon Hill (= HH6–7 of Bosma, 1974). *S. ehingensis* is represented by three $M^{1/2}$s slightly larger than those from Lacey's Farm Quarry, whilst *S. fraasi* is represented by three DP^4s, one $M^{1/2}$ and one $M_{1/2}$ (Figs 24–28). The teeth of *S. fraasi* are all significantly smaller than the equivalent tooth types from Lacey's Farm Quarry; moreover, the DP^4s have a greater length/width ratio, equal widths at both paracone–protocone and metacone–hypocone, and larger, more prominent parastyle with lingual notch.

The highest definite record of *S. bosmae* is from HH4. A few teeth from higher up in marly beds at the top of the


S. authodon
S. minimus
S. palustris
S. fraasi
S. bosmae
S. ehingensis

1. DP^4 with expanded protocone, so lingual margin parallel with buccal margin.
2. DP^4 parastyle usually with lingual notch.
3. Mean M$^{1/2}$ length greater than 1·70 mm.
4. Mean M$^{1/2}$ length less than 1·47 mm.
5. M$^{1/2}$ mesostyle very small or missing.
6. Lower molar mesoconid nearly always linked to hypoconid.
7. Loss of P$^4_4$ and retention of DP$^4_4$.
8. DP^4 length/width ratio greater than 1·11.

Fig. 29 Cladogram of species of *Suevosciurus*. Synapomorphies and autapomorphies are indicated by broad bar. See Fig. 16 for synapomorphies of the genus.

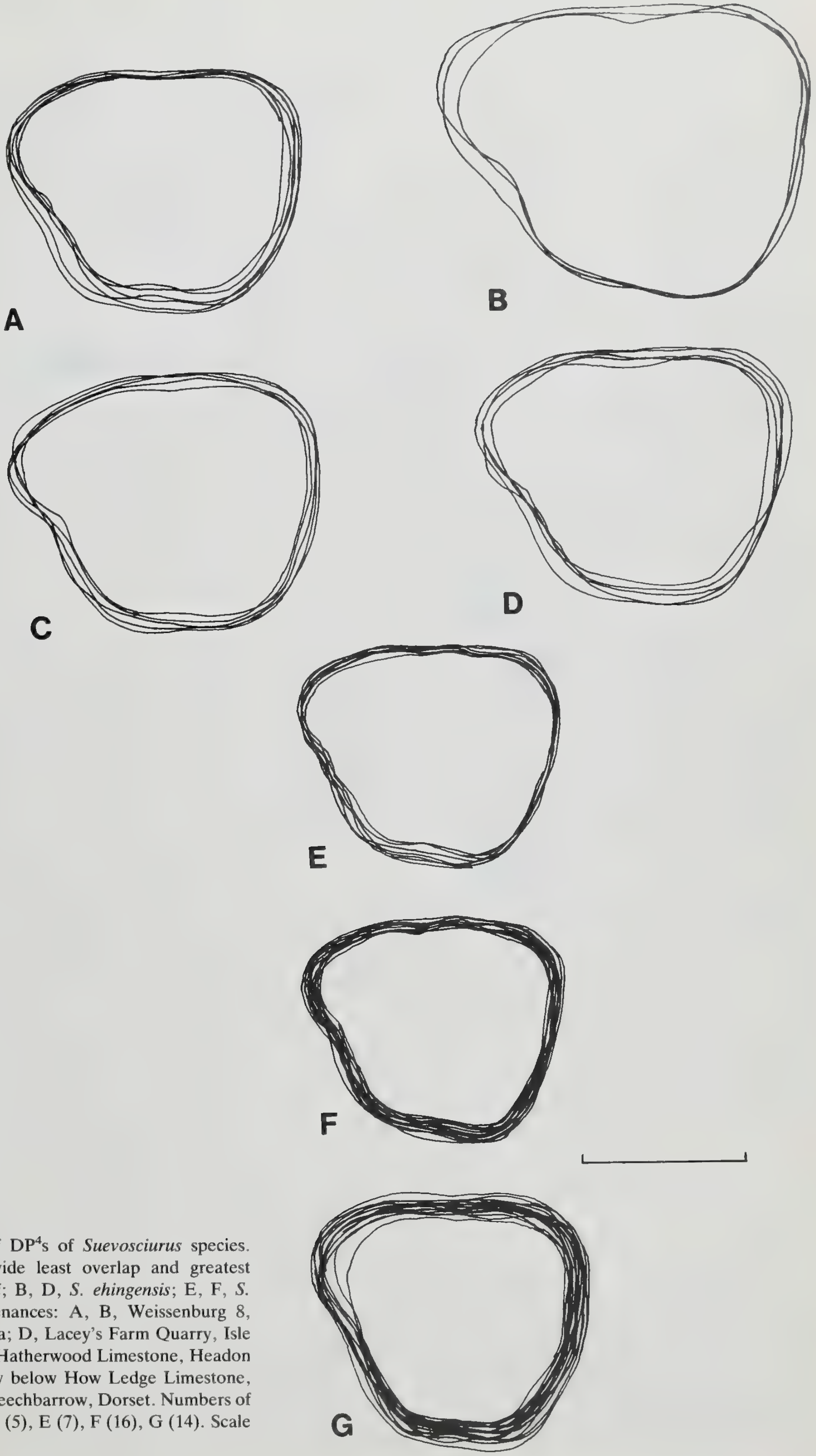


Fig. 30 Superimposed outlines of DP^{4}s of *Suevosciurus* species. Superimposed manually to provide least overlap and greatest shape alignment. A, C, *S. fraasi*; B, D, *S. ehingensis*; E, F, *S. bosmae*; G, *S. authodon*. Provenances: A, B, Weissenburg 8, Bavaria; C, Ehrenstein 1, Bavaria; D, Lacey's Farm Quarry, Isle of Wight; E, base of lignite bed, Hatherwood Limestone, Headon Hill, Isle of Wight; F, green clay below How Ledge Limestone, Headon Hill, Isle of Wight; G, Creechbarrow, Dorset. Numbers of specimens: A (6), B (3), C (5), D (5), E (7), F (16), G (14). Scale bar = 1 mm.

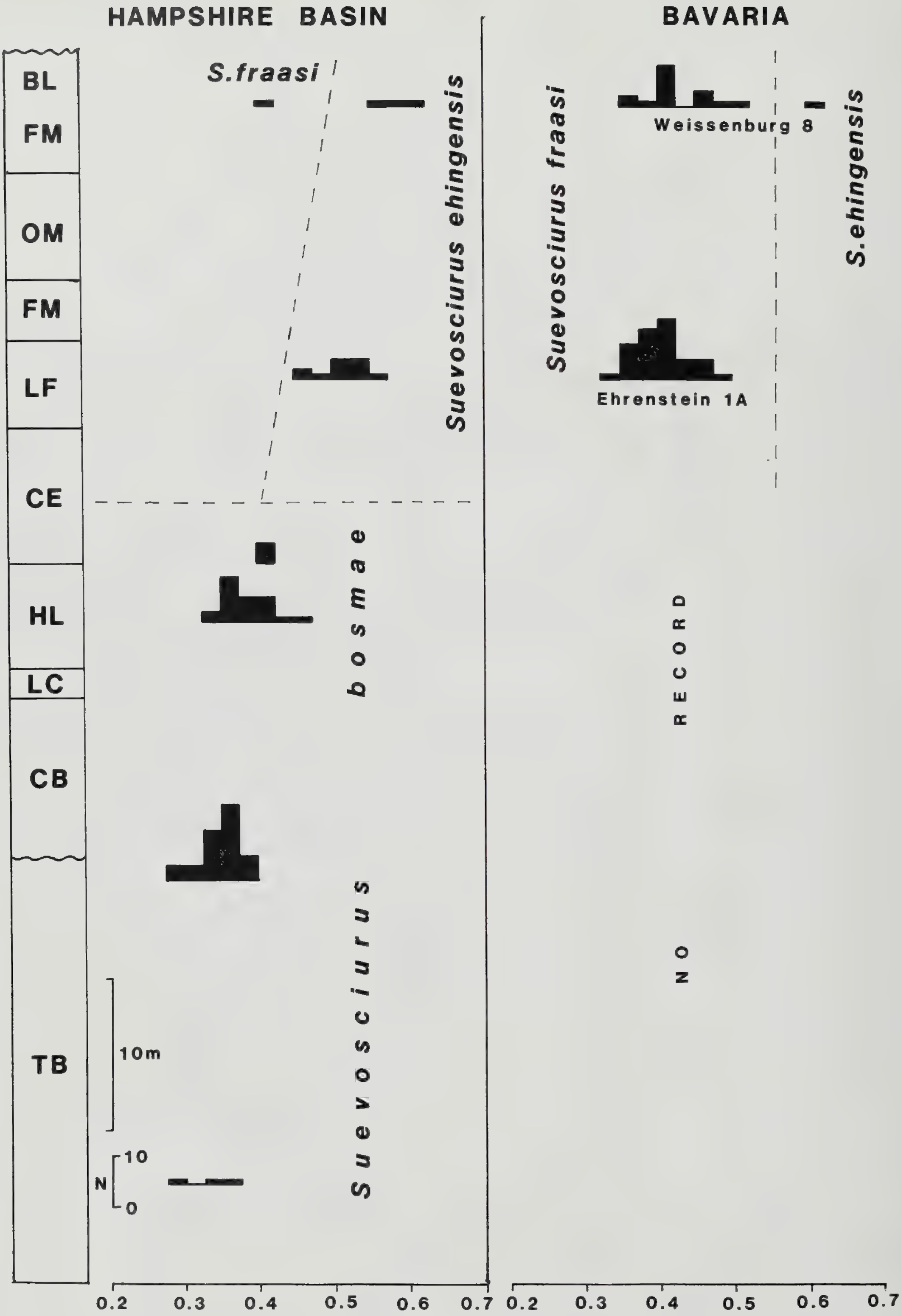


Fig. 31 Histograms in stratigraphic order of $\log_{10}$ (length) × (width) of $M^{1/2}$ of *Suevosciurus* species, from the late Eocene Solent Group sequence in the central Hampshire Basin and relevant fissure fillings of equivalent age in Bavaria, southern Germany. N = number of specimens; m = metres of section; BL FM = Bembridge Limestone Formation; OM = Osborne Marls Member; FM = Fishbourne Member; LF = Lacey's Farm Limestone Member; CE = Cliff End Member; HL = Hatherwood Limestone Member; LC = Linstone Chine Member; CB = Colwell Bay Member; TB = Totland Bay Member. The lower histogram in TB refers to the Hordle Mammal Bed.

Hatherwood Limestone Member of slightly larger mean size (Fig. 31) may represent *S. bosmae*, but the sample as yet lacks the distinctive DP^4. The next record of a *Suevosciurus* is of *S. ehingensis* from the Lacey's Farm Limestone Member, penecontemporaneous with the earliest record of *S. fraasi* at Ehrenstein 1. The evidence available suggests that the speciation event took place within the time represented by deposition of the intervening Cliff End Member at Headon Hill and may have resulted from isolation of populations in the southern English and Bavarian areas respectively. At some time after the deposition of the Lacey's Farm Limestone, and before deposition of the Bembridge Limestone, renewed dispersal to both areas became possible. Species distribution patterns in other genera of mammals from this sequence do not point to other contemporaneous speciation events, although from at least this time until well into the Oligocene, Bavaria had largely endemic faunas (Schmidt-Kittler & Vianey-Liaud 1975; Heissig 1978), and the earlier northern European region as portrayed by Franzen (1968) was split into two by Schmidt-Kittler & Vianey-Liaud (1975), with the boundary at the Rhine Graben. Ziegler (1982) records the Rhine Graben as a site of vulcanism and marine transgression in the late Eocene, which may well have been the isolating mechanism for the *Suevosciurus* speciation. If so, however, it did not prevent the newly formed species from migrating subsequently in both directions.

Speciation patterns

Cladogenetic speciation events have been recorded for several groups of manmals in the dense early Eocene record of the Bighorn Basin, Wyoming, U.S.A., in addition to the more obvious anagenetic events (e.g. Gingerich 1974, 1976, 1977, 1980; Gingerich & Simons 1977). In most cases, however, as one traces two lineages back in time, it is possible to follow only one of them right to an ancestral species, although the pattern of change implies derivation of both from a common ancestor (e.g. Gingerich 1976). A similar pattern has also been described for European Eocene primates (Godinot 1985). At first described as parapatric, this type of cladogenetic speciation was later considered to be allopatric, but where most of the morphological differentiation took place subsequently anagenetically and sympatrically (Gingerich 1977: 491–493). An important problem, however, remains: the lack of similarly dense fossil sequences in areas outside the Bighorn Basin, where the missing branch segment might be represented. Although the late Eocene/early Oligocene mammalian record in Europe is not as dense as in the early Eocene of the Bighorn Basin, and although the sequence in Bavaria is based on biostratigraphy of other mammals, not on superposition, a roughly equal resolution of mammalian faunal succession is recognizable in two European areas. Moreover, in each, it is possible to trace the two lineages of *S. fraasi* and *S. ehingensis* back in time until the former appears in southern England and the latter appears in southern Germany. Earlier than this in the late Eocene of southern England, only a single species (*S. bosmae*) occurs, which is primitive with respect to both *S. fraasi* and *S. ehingensis*. The pattern envisaged here is consistent with a more traditional idea of allopatric speciation, where geographic isolation results in morphologic as well as genetic differentiation before remixing of populations (the 'dumbbell' model – White 1978; Mayr 1982). It may simply have happened that isolation time lasted longer here. Alternatively, smaller population sizes in Eocene 'island' Europe may have produced more rapid character changes. For instance, geographical ranges of some of the critical Bighorn Basin mammals seem to have been large, extending at least from Wyoming to New Mexico (e.g. Gingerich & Simons 1977). The distance between the two European areas under consideration is about 900 km and the maximum area potentially involved (i.e. delimited to the south by a line drawn from Paris to Geneva, as *Suevosciurus* only occurs very rarely further south), judged from palaeogeographic reconstructions (e.g. compilations by Ziegler 1982 and Hooker 1986) is about 300,000 km^2. This is no bigger than the state of Wyoming alone.

It is interesting to note that the newly discovered specimens of *S. fraasi* and *S. ehingensis* in the Bembridge Limestone tend to occur at different levels. Moreover, the former is associated with other taxa, such as primates, an apatemyid and a bat, all small forms which suggest a forested environment. In contrast, the latter is associated with other taxa such as the ungulates *Plagiolophus* and *Diplobune*, which suggest a slightly more open environment. This may indicate habitat differences which were directly related to their speciation. Taphonomic study of this sequence in progress may shed further light on this matter.

There are various potential tests for this speciation event. For instance, to find an Ehrenstein 1 stage *S. fraasi* in a Bavarian fissure containing a single-aged fauna would determine which of the two possible ages was right. The undescribed material from Ehrenstein 2, 3 and 6, Herrlingen 3 and Arnegg 3, listed as '*Suevosciurus minimus – fraasi* (Übergangsform)' by Schmidt-Kittler (1977) could provide the answer. Moreover, the finding of even earlier fissures in this area containing *S. bosmae* would support the isolation model. Conversely, the finding of *S. fraasi* in the Lacey's Farm Limestone Member or contemporaneous strata in the Isle of Wight, or of *S. ehingensis* in a fissure filling the same age as the Ehrenstein 1A fauna in Bavaria, would suggest that the speciation pattern was instead like that documented in the Bighorn Basin for, e.g., *Hyopsodus* and *Cantius* (Gingerich 1977).

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Upper Palaeozoic Anomalodesmatan Bivalvia

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Synopsis. The systematics of the Late Palaeozoic Anomalodesmata (Bivalvia) are considered. Two families, the Sanguinolitidae and Permophoridae, are recognized which are considered to include the ancestors of most of the post-Palaeozoic taxa. They are united by the presence of periostracal spicules in many species of both families, which we regard as a synapomorphy. The new genus *Gilbertsonia* is recognized in the Sanguinolitidae and the two new genera *Siliquimya* and *Bowlandia* are described in the Permophoridae. The Grammysiidae are considered to be a paraphylum which includes the stem group of the Sanguinolitidae. The new Subfamily Cuneamyinae is recognized within the Grammysiidae. We retain three other family group taxa in the Anomalodesmata, the Orthonotidae, the Solenomorphidae (tentatively including a new Subfamily Promacrinae) and the Edmondiacea, which are better placed there than elsewhere, but we have difficulty finding reliable synapomorphies linking them to mainstream forms. Of these three families, we only have evidence that the Solenomorphidae survived beyond the Palaeozoic. Various Upper Palaeozoic Anomalodesmata demonstrate development of a posterior gape, a deep pallial sinus or elongation of the shell, which (by analogy with living taxa) indicate the development of deep sessile burrowing, while other taxa are interpreted as shallow infaunal, slightly mobile burrowers or infaunal nestlers. Some we interpret as crevice dwellers, cavicolous or even epifaunal. The Anomalodesmata reached a high degree of species diversity in the Upper Palaeozoic, with the result that among infaunal bivalves they were commonly the most species numerous bivalve subclass. This species diversity has subsequently increased only gradually, at a much slower rate than other infaunal bivalves. They are now commonly outnumbered by the Lucinacea, Mactracea, Veneracea and Tellinacea in many shallow marine habitats. All Upper Palaeozoic Anomalodesmata have a parivincular, opisthodetic ligament mounted on nymphs which, in conjunction with elongation of the animals posterior to the umbones, leaves the distal part of the dorsal shell margin joined only by periostracum, best interpreted as primitively present rather than the result of secondary fusion. The hinge systems have few or no hinge teeth. No Palaeozoic anomalodesmatan has as yet been discovered with an internal ligament, typical of a number of Mesozoic and surviving lineages.

INTRODUCTION

During the last two decades understanding of the morphology and ecology of Upper Palaeozoic bivalves (pelecypods) has developed rapidly and, in particular, the understanding of the adaptation of form to burrowing habits and the ancestral relationship of Mesozoic forms. An early analysis by Newell (1956) was followed by the work of Runnegar (1965, 1966, 1967, 1968, 1974), Waterhouse (1965, 1966, 1969*a*, 1969*b*) and Runnegar & Newell (1974). Astafieva-Urbaitis has extensively examined the morphology and relationships of Carboniferous forms (1962, 1964, 1970, 1973, 1974*a*, 1974*b*), and Muromzeva has described both Carboniferous and Permian taxa from the Soviet Arctic (1974, 1984).

The present paper examines the morphology and relationships of forms which have been referred to *Sanguinolites* M'Coy 1844, and *Allorisma* King 1844, and their relationships to each other and to younger forms are considered. (Hind (1900: 311) referred these genera to the Family Coelonotidae M'Coy 1855. The family name Caelonotidae (not Coelonotidae) was used by M'Coy (1852: 275). The name Caelonotidae is apparently unavailable as it is not based on a valid generic name (I.C.Z.N. Art. 11 (e)), as observed by Runnegar (1967: 27)). Our work should be considered within the overall framework presented by Runnegar & Newell (1974) and Runnegar (1974). One group of species, which for the present is referred to *Pleurophorella* Girty (1904), is shown to be readily separable and should be placed in the Family Permophoridae. Hitherto, this family has been placed in the Superfamily Carditacea; in this paper its position there is regarded as unlikely as is also its relationship with the heterodonts. Other forms are placed in the

Edmondiidae and Sanguinolitidae and their family relationships are discussed.

Astafieva-Urbaitis (1974*a*) has investigated the relationships of species placed in *Sanguinolites*. She concluded that a number of distinct groups have been included in the genus *Sanguinolites*. We agree with her conclusions, and we make further proposals to help in resolving this problem, based on the examination of the extensive collections in the British Museum (Natural History), London, including Hind's material. Astafieva-Urbaitis (1974*b*) also discussed the characters and relationships of *Praeundulomya*, which she concluded was related to *Wilkingia*, and she placed it within the Family Sanguinolitidae. In 1973 she had proposed the Subfamily Undulomyinae (of the Sanguinolitidae) for *Wilkingia, Praeundulomya*, and *Undulomya*. In 1983 with Dickins she introduced a new name *Dulunomya* for species which they regarded as morphologically intermediate between *Wilkingia* and *Praeundulomya*. Here we reassess these genera based on their type species and include *Exochorhynchus*. We consider a taxon in this subfamily to be ancestral to *Pholadomya*.

SHELL STRUCTURE

In common with the living Anomalodesmata, the shell thickness of the Sanguinolitidae is variable: it is thin in *Sanguinolites* and *Wilkingia* and rather thicker in *Pleurophorella*. Most species of these genera have a pustulose surface. In the more spectacular forms the pustules are calcareous spikes (Aller 1974), which occur in *Wilkingia, Praeundulomya, Pholadella, Cimitaria* and *Chaenomya* where they are arranged in prominent radial rows. In *Pleurophorella striatogranulatus* they are better described as pustules.

Periostracal calcareous structures occur in several groups of bivalves (Carter & Aller 1975) but are not clearly present in all the taxa we consider to belong to the Anomalodesmata; this may sometimes be due to lack of preservation or sometimes their real absence. Where they do occur, however, in spike-like form, we consider that they indicate that the taxa possessing them do belong to the subclass. We consider the absence of periostracal calcareous structures in certain Anomalodesmata to be a character of taxonomic value at a level lower than subclass.

Periostracal calcareous structures are very uncommonly preserved in the Edmondiacea. Their presence in one species of the Family Megadesmidae (Runnegar 1965) and in Russian specimens of the genus *Allorisma* (Astafieva-Urbaitis & Dickins, personal observation) leads us to accept the inclusion of the superfamily within the Anomalodesmata. Other records of calcareous surface spicules that we have checked in the Edmondiacea have proved to be spurious. Pustules are also unknown in the Orthonotidae, a fact which supports the view that they should not be included within the Pholadomyoida.

Spicules are clearly preserved in *Pachymyonia* cf. *occidentalis* Dickins (1963: pl. 5, fig. 20) from the Permian Fossil Cliff Formation of Irwin River, West Australia, but this species may be related to *Sanguinolites argutus* Phillips, from the Viséan of Britain, rather than the Megadesmidae. Wilson (1960: 111) recorded fine, close-set striae radiating from the umbones of *Edmondia sulcata* (i.e. *Allorisma sulcata* of this paper). He considered these to be internal representatives of the rows of minute tubercles on the exterior of the shell illustrated by Hind (1899: pl. 35, fig. 11a). Hind's piece of shell, however, is apparently a *Wilkingia* and the radiating striae seem to be concerned with the attachment of the mantle to the shell and not connected with external pustules.

We have been able to study the shell structure in just one species, *Myofossa costellata* (M'Coy, 1851*a*) where an internal nacreous layer is perfectly preserved (Fig. 1). A very thin outer layer is less well preserved and is in a blocky, recrystallized form, but we have been able to interpret it by its general appearance as a thin prismatic outer layer that was originally aragonite. A simple thin myostracal layer of short aragonite prisms was identified, as in other Mollusca.

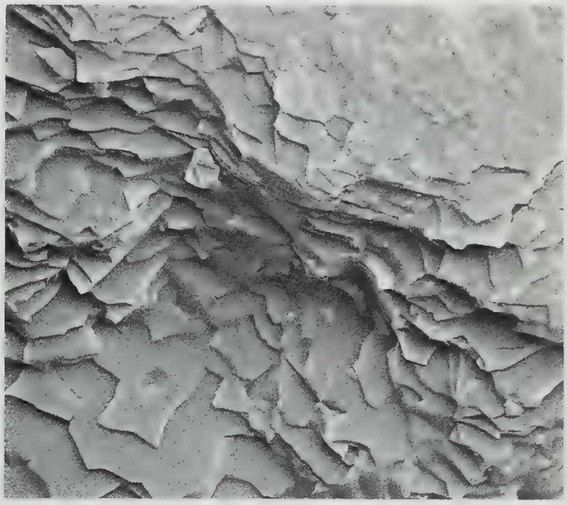


Fig. 1 Nacreous shell structure of the inner ostracum of *Myofossa costellata* (M'Coy); BM L46425, oblique stereoscan view of broken shell, ×720; see also Fig. 12d.

We suspect that the calcareous shell of the Sanguinolitidae consists of an outer layer of aragonite prisms, usually with a pustulose surface, and an inner layer of nacreous structure subdivided by a sheet of myostracum. This combination of aragonite prisms with an inner nacreous layer is generally considered primitive for the Mollusca (Taylor 1973), and we believe it to be the primitive condition of the Anomalodesmata. We consider that non-nacreoprismatic shells have evolved on several separate occasions in the descendants of the Palaeozoic Anomalodesmata. Intermediate stages are recognized in the Myopholadidae which we interpret as early representatives of the Pholadidacea (Taylor, Kennedy & Hall 1973). The nacreous layer may have given rise to homogeneous structure in the Ceratomyidae, although this structure could already have been present in the Edmondiidae and the Solenomorphidae, one species of which may have been their ancestor. This may also have happened in the Pleuromyidae and their descendants such as *Panopea*, and in *Gastrochaena* and *Myoconcha*, It may also have evolved later into cross lamellar structure in the Myopholadidae and Myidae.

In the Corbulacea, crossed and complex crossed-lamellar structure may also have evolved from the primitive anomalodesmatid shell, but an alternative possible derivation of this group is from the heteroconchs *via* the Myophoricardiidae. *Myopholas* and some species of *Panopea* retain the outer layer of aragonite prisms complete with pustules, at least in their early growth stages, but these are lost in the later Pholadacea, the Myidae and *Hiatella*.

HINGES

We have examined well-preserved hinges in several species of *Sanguinolites, Pleurophorella, Myofossa, Wilkingia* and *Chaenomya* and have compared them with the better known hinges of the Edmondiidae, Permophoridae, Megadesmidae and the post-Palaeozoic Anomalodesmata. The sanguinolitid dorsal margin is usually straight and long, the valves being in juxtaposition from just in front of the umbones to a point above or just posterior to the posterior adductor scar. Nymphs are present, but are normally not well developed; their anterior point is immediately below the umbones, and posterior to this point (Figs 6, 9, 12, 13, 32) they vary from short to long.

We have observed ligament material only in *Pleurophorella* sp., *Sanguinolites costatus, Chaenomya leavenworthensis* and *Edmondia* sp. Ligaments have previously been described in the Megadesmidae (Runnegar, 1968). In that family the ligament does not extend posteriorly very far from the nymph. Runnegar recognized a small extension to the ligament beyond the partly fibrous ‘C spring’ ligament mounted on the nymphs. In his text-figure 1a he calls this the ‘fusion(?) layer’, following the interpretation of modern ligaments by Yonge (1957), Owen, Trueman & Yonge (1953) and others. In the Edmondiidae (Waterhouse 1966, Runnegar & Newell 1974) the ligament nymph is relatively more elongate.

The Upper Palaeozoic taxa here included in the Pholadomyacea have a limited range of ligament types. All have structures which are properly described as nymphs; a number of species have the remains of ligament attached to these nymphs. In what we interpret as the more primitive forms, the nymph is set in a clearly defined escutcheon, usually set between dorsal carinae, which extends from the initial growth point between the umbones to the posterior dorsal corner of the shell. In most of these taxa the dorsal margins within the escutcheon are straight and come into close contact with each other, whether the valves are preserved in the live open or closed position. In such forms we consider that the periostracal covering of the ligament continued beyond the distal end of the nymphs, joining the shells as periostracal ligament. This type of ligament has been termed ‘fusion layer’ by Yonge (1957). However, in the case of these Upper Palaeozoic anomalodesmatans we consider the term to be inappropriate. We consider that this periostracum was not formed by fused mantle edges but was more likely to have been laid down by the original, primitive dorsal skin of the animal. It may have been deposited initially by the inner surface of the outer mantle fold at the posterior of the shell and then thickened by the outer surface of the skin along the dorsum. The dorsum and the periostracal ligament may have been extended from a more primitive shorter state by posterior hypertrophy of these elongate infaunal animals.

Modifications of the primitive ligament pattern that occur in the Upper Palaeozoic Anomalodesmata include the presence of nymphs where the lamellar and fibrous ligament layers are attached. In a hypothetical, simplest form, all the layers of the ligament would extend approximately the same distance distally along the dorsum. This arrangement occurs today only in the Mytilacea, where it is modified by the peculiar nature of the calcareous material joining the ligament to the shell. In all the Pholadomyacea we have studied, the distinct nymph does not run to the end of the escutcheon. The nymph is usually relatively short in the taxa we interpret as having been entirely infaunal; this condition occurs in *Grammysioidea, Sedgwickia*, and *Chaenomya*. It is slightly longer in the Undulomyinae, longer still in *Sanguinolites*, and quite long in many of the Permophoridae, which include species we would interpret as only semi-infaunal, byssally attached nestlers. Some Gastrochaenacea have reduced the length of the nymph from that of their permophorid ancestors. *Spengleria rostrata* (Spengler), from St Thomas, has a broad short nymph, whereas *Gastrochaena mytiloides* (Lamarck) from Mauritius has an elongate ligament set in a notch along the top of the hinge, suggesting that the length of the ligament may be highly adapted to slight differences in life style and might not always reflect phylogeny.

The Edmondiacea also have a relatively long ligament nymph (Runnegar & Newell 1974) which may be a primitive

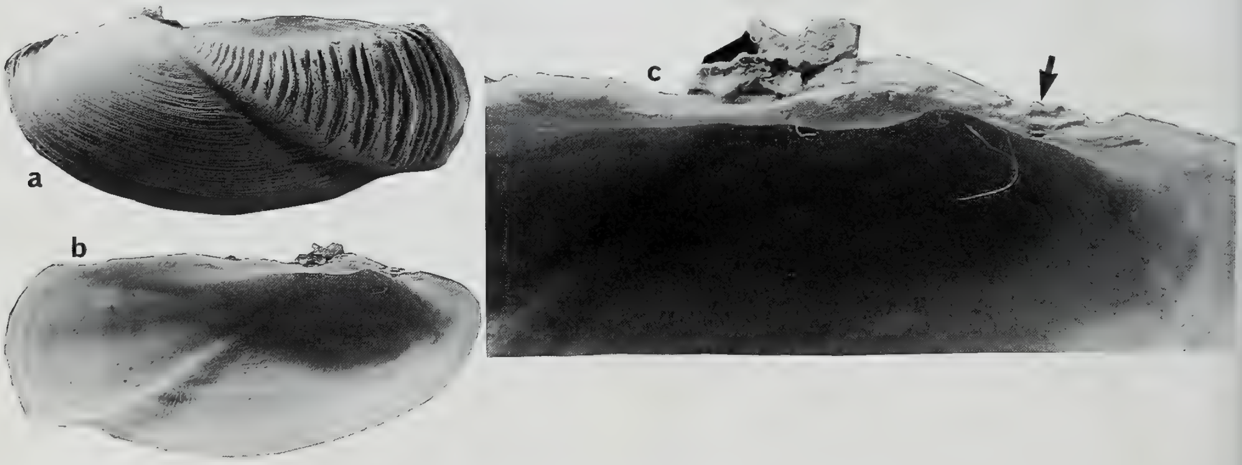


Fig. 2 *Spengleria rostrata* (Spengler). Recent, St Thomas I., Caribbean. BM (ZD) unnumbered (Cuming Collection, *ex* Dr Hornbeck). Figs 2a, 2b, exterior and interior view of left valve, slightly enlarged. Fig. 2c, interior view of dorsal margin of left valve, showing the development of ridges anterior to the umbones due to the emplacement of anterior fused periostracum (arrowed), ×6.

character for that superfamily. Some Sanguinolitidae, as well as the majority of species of *Pholadomya*, develop a marked permanent posterior gape for the siphons. By comparison with living taxa, such large gapes are invariably accompanied by fused siphons of type 'C' (Yonge, 1957). In *Chaenomya* the gape extends along the posterior part of the dorsal margin. The escutcheon is partly lost and it is clear that the dorsal margins behind the nymphs were not continuously joined by periostracal ligament. We take this to be an advanced character, associated with largely or at least partly retractile siphons.

In *Spengleria rostrata* the valves are joined by periostracum anterior to the umbones. In dead shells the anterior dorsal margin has a chalky texture with layers of periostracum along the shell margin (Fig. 2). This clearly resembles, and we consider it to be analogous to, the structure figured by one of us (Astafieva-Urbaitis 1964) in a species of *Allorisma*, where it was suggested that they may be anterior teeth.

SYSTEMATIC DESCRIPTIONS

Abbreviations. Specimens in the following institutions are referred to in the text and figure captions with the following abbreviations:

BGS	– British Geological Survey, Keyworth, Nottingham.
BM	– The Natural History Museum, Cromwell Road, London (formerly the British Museum (Natural History)).
BMR	– Bureau of Mineral Resources and Mines, Canberra.
EMP	– École des Mines, Paris (now at Université de Lyon, France).
GSI	– Geological Survey of India, Calcutta.
NMI	– National Museum of Ireland, Dublin.
SM	– Sedgwick Museum, Cambridge.
USNM	– United States National Museum, Washington.
MNHN	– Musée Nationale d'Histoire Naturelle, Brussels.

Subclass **ANOMALODESMATA** Dall, 1889

The Upper Palaeozoic taxa included in this subclass are listed on p. 92. We describe here representatives of the Edmondiacea and Pholadomyacea. What we interpret as primitive characters within the subclass include an equivalve nacreoprismatic shell composed entirely of organic material and aragonite, joined across the dorsum by a three-layered, opisthodetic, parivincular ligament mounted on narrow but distinctive nymphs. More or less isomyarian adductor muscles are joined by an entire pallial line. We are uncertain whether the most primitive Anomalodesmata possess simple hinge teeth or have none. We regard the possession of spicules of aragonite on the shell surface set within the periostracum as a synapomorphy of the Anomalodesmata, but we are prepared to modify this view if a sister group of the extant representatives is recognized which did not develop this feature. We consider it unlikely that the view expressed by Carter & Aller (1975), that these periostracal spicules are the homologue of similar structures in chitons and therefore a primitive character of the Mollusca, is correct. Most Anomalodesmata have somewhat elongate shells, which we consider to be primitively infaunal, often with modification of the form of the posterior margin, which suggests that the inhalant water current of the mantle cavity was posteriorly placed. This may not be the case in primitive edmondiaceans. A subumbonal sulcus is present in many anomalodesmatans and may indicate the anterior limit of ventral mantle fusion.

Pojeta (1971) has excluded the family Orthonotidae from the Anomalodesmata, suggesting first that they should be allotted to a separate Order Orthonotoida (Pojeta 1978), but he later suggested an affinity with the Mytiloida (Pojeta, Zhang & Yang 1986). On all occasions, and with support from Runnegar (1974), the similarity between the Orthonotidae and the living Solenacea was stressed by these authors. A separate (unpublished) study (N.J.M. *in litt.*) supports an alternative view that the Solenacea are more closely related to the Tellinacea, and both superfamilies probably arose from an ancestor currently classified with the Tancrediidae. We suggest that the *Solen*-like shape has arisen at least four times throughout bivalve evolution; once within primitive Ordovician forms of uncertain affinity, once in the Orthonotidae, once in the Quenstedtiidae and at least once in the Solenacea. We consider all these cases to be due to convergence. The significance of the Orthonotidae to the classification relates to our inablility to decide, on the presently available evidence, whether the Devonian to Triassic family Solenomorphidae is more closely related to early Devonian Sanguinolitidae such as *'Leptodomus' acutirostris* (Sandberger) (Beushausen, 1895: pl. 24, figs 8–10) or to *Orthonota*. Bittner (1895: pl. 1) illustrated a series of species of *Solenomorpha* from the Carnian of northern Italy which grade insensibly into what seem to be the earliest representatives of the Cuspidariidae. Interpretation of their ancestry will indicate whether or not the Cuspidariidae are properly placed in the Anomalodesmata. The shell shape, differentiation of a corselet and subumbonal sulcus, all typical of species of *Orthonota*, are not characters of the Mytilacea. However, until a well-preserved hinge is described for that genus, its systematic position remains debatable.

We include provisionally a new Subfamily Promacrinae (p. 93) within the Solenomorphidae. *Promacrus* is superficially similar to the living arcacean *Litharca*, but apparently does not have an arcid hinge. Many of the species have an opisthodetic parivincular ligament with the umbones well to the posterior, and are similar in this respect to the Solemyidae. However, a specimen of *Promacrus* in the United States National Museum labelled *Promacrus undatus* Ulrich MS, from the Lower Cuyahoga Shale of northern Ohio, has a clearly preserved anterior adductor scar, which does not impinge upon the body attachment scars in the way peculiar to the Solemyidae. In addition we take the condition of *Promacrus websterensis* as originally illustrated by Weller (1899; 34, pl. 2, figs 2–7; pl. 3, fig. 1), where the umbones are more medially placed, as primitive for the genus and subfamily, and therefore less similar to the solemyid shape. We provisionally place the Promacrinae in the Solenomorphidae but feel this view may have to be modified when the hinge of *Promacrus* is adequately described.

The Prothyridae are another difficult family to place with certainty, but in Driscoll's illustration of the surface sculpture (Driscoll, 1965: pl. 11, figs 1–9), the fine radial striae resemble similar structures in a number of Mesozoic Anomalodesmata. Although carbonate spicules are not preserved in *Prothyris* a relationship to the Anomalodesmata is indicated.

Superfamily **EDMONDIACEA** King, 1850

The Edmondiidae include three oval genera, *Edmondia*, *Scaldia* and *Cardiomorpha*, which are more or less isomyarian with an entire pallial line, and a more elongate genus *Allorisma*. *Edmondia*, *Scaldia* and *Allorisma* share an internal rib below the hinge plate which is not usually well developed in species of *Cardiomorpha*. The Edmondiacea share only primitive characters with the other Anomalodesmata, except for the rare occurrence of periostracal spicules. All the other characters we are able to recognize, we would expect to be primitive in early members of the Heteroconchia. The superfamily is placed within the Anomalodesmata largely by tradition. However, by assuming the periostracal spicules are a synapomorphy for the Anomalodesmata as a whole we support their inclusion in this subclass. At present we find no irrefutable evidence for the occurrence of edmondiaceans before the latest Silurian, but we suspect that earlier representatives will be either recognized or confirmed.

The rounded edmondiid shell with its regularly curved pallial line is consistent with a mantle cavity lacking a specialized channelling for the inhalant current. We consider the more elongate form and more intricate musculature of *Allorisma* to be advanced features. This lack of channelling of the inhalant current might have been similar to that of primitive living Veneroida such as *Astarte* and nuculoids such as *Nucula*, and may well have been primitive for the Lucinoida. Unlike representatives of the latter order, no edmondiid or conceivable relative discussed below, megadesmid, mactromyid or poromyid, has the hypertrophied anterior adductor scar of the Lucinacea, which is clearly visible in the earliest certain lucinacean, *Ilionia* (from the Silurian of northern Europe).

We include two Palaeozoic families in the Edmondiacea, the Edmondiidae and the Megadesmidae. The Edmondiidae are found mainly in strata of Devonian to Permian age, laid down in temperate and warm seas, now in the northern hemisphere, whereas the Megadesmidae mainly occur in the cold and cold-temperate waters of the southern hemisphere of Permian times. De Koninck (1877–8) distributed his new species from the Permian of Australia, now recognized as belonging to *Megadesmus*, among his own genera *Edmondia* and *Cardiomorpha*. Although the megadesmid genera from Australia have a characteristic shape, a relatively larger size, immensely thicker shells and more robust ligaments than Carboniferous species of *Edmondia* and *Cardiomorpha*, the similarity implied by de Koninck is real. The relationship has been widely discussed and has been summarized by Runnegar (1967: 29). We have compared the shell shape and hinge structure of a young specimen of *Megadesmus grandis* (Dana) and the musculature of several specimens of *Astartila intrepida* (Dana), both from the Illawara District of New South Wales, Australia, with the same features of a well-preserved Lower Namurian English specimen of *Cardiomorpha obliqua* Hind, and find no significant differences. Unlike *Edmondia, Scaldia* and *Allorisma, Astartila* and *Megadesmus* have no significant internal rib on the hinge plate. We know of no taxon more similar to these megadesmids than *Cardiomorpha obliqua*, and interpret that species as the closest known relative to the Megadesmidae. We have noted the superficial similarity in shape and sculpture between *Cardiomorpha* and the Jurassic genus *Ceratomya*. Both have a similar size, globose form and comarginal ribs, which has led Runnegar to speculate (1974: text-fig. 3) that *Ceratomya* evolved from the edmondiids and occupied a deeper burrowing habitat, signified by the acquisition of a pallial sinus. *Ceratomya* also developed an internal ligament by overlap of the left nymph by the right valve, and further has homogeneous rather than nacreoprismatic shell structure. Our greatest misgiving, however, is in the shell morphology of the oldest genus we attribute to the Ceratomyidae and which we would interpret as the primitive morphology of that family. This is the Rhaetian to Hettangian genus *Pteromya*, which is more elongate and less gibbous than any *Cardiomorpha* or *Edmondia*. At present we are impressed by the external similarity between the sculpture of *Pteromya* and that of Middle Jurassic species of Cuspidariidae, and we conclude that the similarity between the gibbous shells of *Ceratomya* and *Cardiomorpha* is a consequence of convergence.

The question still arises as to whether the Edmondiacea survived beyond the end of the Palaeozoic. At an early stage we thought that the Corbulacea (Mesozoic to Recent) were derived from the Megadesmidae (outlined in Taylor *et al.* 1973, final chapter). However, we now favour a relationship between the Corbulacea and the Crassatellacea, particularly the Triassic family Myophoricardiidae. We consider the similarity of hinge structure between the Corbulidae and the Myidae to be best interpreted as a case of convergence. It is hoped to enlarge on this hypothesis in a later paper.

It has been suggested by Runnegar & Newell (1974) that the late Triassic genus *Ochotomya* Kiparisova *et al.* 1966 may have evolved from a megadesmid ancestor. It is possible that *Ochotomya* is an early representative of the Poromyacea. We can find no authentic poromyacean earlier than the Late Campanian; we include the *Liopistha* group in the Cardiacea on the basis of their cardinal teeth, shell structure and muscle scars. In spite of the considerable time gap between the Late Triassic and the Campanian we have so far been able to suggest no more plausible relationship for the Poromyacea. However, *Bowlandia* sp. (Fig. 45) is an equally plausible relative for *Ochotomya*. The basis for separation of the Edmondiacea is discussed under Pholadomyacea. Here we note the considerable convergence between the genus *Allorisma* of the Edmondiidae and genera of the sanguinolitid Subfamily Undulomyinae. They are distinguished by the pattern of the accessory musculature and the presence of the hinge plate rib which appears to be a synapomorphic character of a number of Edmondiidae, although it may be lost during the course of later evolution. The possibility arises that the Mesozoic genus *Mactromya* and its relatives are descendants of the genus *Edmondia*, and that the Edmondiacea as a whole are better placed in the Heteroconchia. We are uncertain whether the subumbonal hinge teeth present in the edmondiid genus *Scaldia* and the Mesozoic genera *Sphaera* and *Schafhaeutlia* are an advanced or primitive character for the group. We have been unable to ascertain the shell structure of Palaeozoic Edmondiacea. In the Upper Pennsylvanian of Texas an unnamed species occurs in a preservation similar to that which has yielded shell structure information in some other taxa; only the growth laminae were clearly preserved. It is possible that the inner layer was nacreous but it is not sufficiently well preserved for us to be certain. Runnegar (1967: pl. 6, fig. 12) has illustrated what appears to be the nacreo-prismatic shell of the genus *Megadesmus*. The Lower Jurassic *Mactromya cardioides* (Phillips), from the Lower Pliensbachian, Luridum Subzone of Blockly, Gloucestershire, England, shows clear aragonite crossed lamellae and some finer structure that was apparently of amorphous type. This shell structure does not conflict with our view that the Mactromyidae may be closely related to the Lucinacea. Further work is necessary to decide whether the similarity of the Edmondiidae to the Mactromyidae is the result of convergence or descent.

Family **EDMONDIIDAE** King, 1850

Genera referred here to this family are *Edmondia, Allorisma, Scaldia* and *Cardiomorpha*, which all possess a hinge plate reinforced internally by a ridge or lamellar plate projecting into the shell cavity; it is equivalent to the 'internal cartilage plate or ossicle' (Wilson 1960, Waterhouse 1969*a*, Runnegar & Newell 1974). Earlier, one of us (Dickins 1963) had suggested that the Megadesmidae might be included in the family Edmondiidae, but this relationship has been discussed by Runnegar & Newell (1974), who showed that *Allorisma, Scaldia* and *Cardiomorpha* also had an internal lamellar plate as well as having other characters in common with *Edmondia*. On the basis of this information and further data presented here we also conclude that the Edmondiidae and the Megadesmidae should be recognized as separate families. Edmondiids from western Europe such as *Cardiomorpha obliqua* Hind (1898: 263) and *Edmondia lyellii* Hind (1899: 300) are the most similar to typical Australasian genera *Megadesmus, Pyramus* and *Astartila*. We imagine the ancestry of the Megadesmidae to have been from taxa such as these. *Cardiomorpha obliqua* in particular is thick-shelled for an edmondiid. Although its hinge margin is quite thick, the internal rib is only just distinct and its adductor and accessory muscle scars are rather similar to those of the megadesmids. We suspect that the species of *Vacunella, Australomya* and *Myonia* from eastern Australia are true anomalodesmatids, which are not necessarily closely related to the megadesmids. Periostracal spicules are not usually preserved on the shell surface of Edmondiacea, but Runnegar (1965: pl. 13, fig. 9) clearly illustrates their presence in *Megadesmus gryphoides* (de Koninck). We are unable to say whether they originally occurred on other taxa within this superfamily.

We follow Astafieva-Urbaitis (1964) and Runnegar & Newell (1974) in separating *Allorisma* from *Edmondia* and add some further information on the musculature of *Allorisma*. *Scaldia* can be separated, as it possesses a hinge tooth, and *Cardiomorpha* includes slender to inflated circular shells with inrolled umbones. The Edmondiidae were apparently shallow burrowers and did not develop in the same area as the Megadesmidae. The Edmondiidae are found mainly in strata laid down in temperate and warm seas of the northern hemisphere, whereas the Megadesmidae mainly occur in the cold and cold temperate waters of the southern hemisphere.

Genus ***ALLORISMA*** King, 1844: 315
Fig. 3

Type species. *Hiatella sulcata* Fleming (1828: 462) by subsequent designation of King (1850: 196, footnote 6) (not *Cardiomorpha sulcata* de Koninck, 1842, which is not an *Allorisma*).

Wilson (1960: 114) and Newell (1969: N818) considered

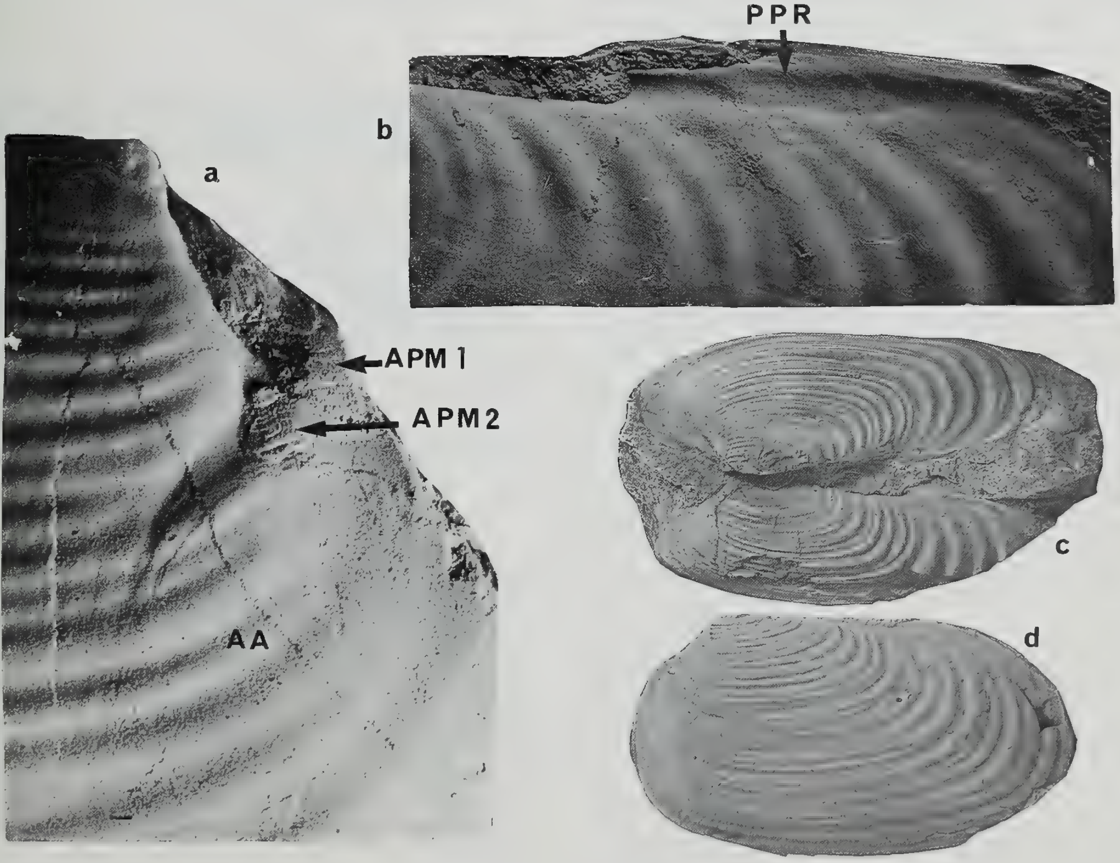


Fig. 3 *Allorisma sulcata* (Fleming). Carboniferous. Figs 3a–b, Lower Namurian, Main Limestone, Stanhope, Northumberland; BM PL5000, Trechmann Collection. Fig. 3a, anterior of right valve with anterior adductor AA, and two anterior pedal-body attachment scars APM1 and APM2; Fig. 3b, posterior dorsal area of left valve with attachment scar or posterior pedal retractor PPR. Figs 3c–d, Viséan, Ballasalla, Isle of Man; BM L45456, dorsal and side views, ×1.

Sanguinolaria sulcata Phillips 1836 to be the type species of *Allorisma* by original designation of King (1844: 313). In his original description of *Allorisma*, however, King mentions several species and only in the letter of introduction to his paper does he refer to the new genus '*Allorisma* for species represented by *Sanguinolaria sulcata*. Ph'. This does not seem to represent an explicit designation of type species, whereas in 1850 King made a definite designation. Wilson (1960: 112) chose a lectotype for *Hiatella sulcata* Fleming from amongst Fleming's specimens, and presented evidence that *Sanguinolaria sulcata* Phillips 1836 should be regarded as a synonym of *Hiatella sulcata* Fleming 1828.

SYNONYMS. *Edmondiella* Chernychev, 1950: 74 (type species, *Sanguinolaria sulcata* Phillips 1836 by original designation). *Edmondia* King 1850 *pars* (1850: pl. 20, figs 1–2) (not *Edmondia* de Koninck, 1844).

DESCRIPTION. Thin-shelled, elongate oval, with umbones situated distinctly towards the front. Rather evenly rounded over the surface of the shell and lacking a distinct escutcheon or lunule. Ornament of well developed rounded rugae more or less parallel to the external margin. In internal impressions a smooth area is marked off by the anterior adductor. Has a distinct internal ridge or lamellar plate as in other Edmondiidae. Hinge lacks teeth and apparently with an external opisthodetic ligament. Anterior adductor muscle scar moderately well marked at right angles to margin in front of umbones rather than vertical. Two other separate muscle attachment marks are associated with the adductor (Fig. 3). The longer scar runs parallel to the front part of the dorsal margin and behind has a distinct buttress (clavicle). At the dorsal end of the buttress is the rounded mark of another muscle. The two smaller muscles perhaps represent the pedal protractor and retractor. The posterior adductor muscle is poorly marked but a posterior pedal retractor is visible towards the back of the dorsal margin. Delicate lines radiate from the umbones of external impressions.

REMARKS. The description is largely based on the type species. The elongate shape seems sufficient to distinguish *Allorisma* from *Edmondia*, which, in addition, commonly has lamellate shell ornament not so far recorded in *Allorisma*. Although the anterior accessory muscles are similar in *Edmondia* (Runnegar & Newell 1974) and *Allorisma*, a distinct buttress is not recorded in *Edmondia* nor the muscle impression at the dorsal end of the buttress.

[*Note: Allorisma regularis* de Verneuil (1845: 298; pl. 19, figs 6a–b; pl. 21, figs 11a–b) was attributed by de Verneuil to King out of courtesy. It was, however, never described by King but is referred to by him (King 1850: 196) as described by de Verneuil. The two specimens figured by de Verneuil represent two species. We here designate the specimen figured in de Verneuil, 1845: pl. 19, figs 6a–b as the lectotype, to safeguard the usage of Astafieva-Urbaitis (1962), who was apparently the first revising author. This specimen belongs to the genus *Wilkingia*. The other specimen (de Verneuil 1845: pl. 21, figs 12a–b) has a lamellar plate and belongs to *Allorisma* as used in this paper, and as appreciated by King in his footnote. It is here considered to be a synonym of *Allorisma sulcata*.]

Superfamily **PHOLADOMYACEA** King, 1844

Although the family name Pholadomyidae was used by Gray (1847: 194) (Newell 1969: N818, Runnegar 1974: 425), it was used earlier by King (1844: 315). The name Pholadomyacea is assigned by Newell (1965: 21) to Fleming (1828), but this is apparently an error because Fleming (1828: 424) referred *Pholadomya* to the Cardiadae (*sic*).

In the *Treatise*, Newell (1969) separated the Edmondiidae as a single family in the superfamily Edmondiacea, but Runnegar & Newell (1974) place the family in the Pholadomyacea. In the latter case the name Edmondiacea would become redundant, as also would Grammysiacea, the Grammysiidae being placed in the Pholadomyacea, which has priority over both names. The superfamily has thus become very broad and we have misgivings about including some Palaeozoic genera, which, although generally related to *Pholadomya*, are rather distinctive. Runnegar & Newell and our present work emphasize the significance of the lamellar plate in the Edmondiidae. We consider the muscle attachment associated with the plate would give greater stability and strength to the valves in burrowing. Apparently this feature is a long-standing one, as the lamellar plate is also developed in a Welsh Lower Devonian species, ?*Edmondia* sp. from the Tilestones at Capel Horeb (BM LL31477). We propose to emphasize the significance of this feature by recognizing the Superfamily Edmondiacea to include the Family Edmondiidae.

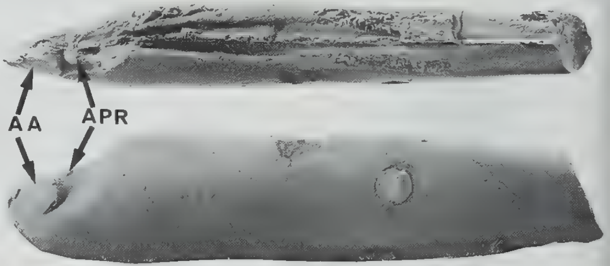


Fig. 4 *Solenomorpha minor* (M'Coy). Lower Carboniferous, Viséan, Yeat House Quarry, Cumberland. BM L47699, Hind Collection (figd Hind, 1904: 159; pl. 22, fig. 3); views of steinkern from the top and left side, showing anterior adductor AA, and anterior pedal retractor APR. ×1.

We place the Sanguinolitidae and the Permophoridae in the Superfamily Pholadomyacea, although this is not altogether satisfactory because these two families are distinct from the rest of the superfamily. Alternatively, to separate a Superfamily Grammysiacea for these two families would seem even less satisfactory. The later representatives of *Grammysia* itself appear to be a group of round-shelled, non-siphonate species for which we can find no evidence of survival beyond the end of the Devonian. We would be reluctant to propose another superfamily without further work and review of pre-Carboniferous and post-Permian bivalve faunas, because the lineages we are discussing and using as a basis of family taxonomy occur in the Carboniferous and later faunas, and this information will allow the establishment of more satisfactory systematics.

Family **SANGUINOLITIDAE** Miller, 1877

Synonym. Caelonotidae M'Coy, 1855, an invalid name according to ICZN Art. 11e (not Coelonotidae).

Remarks. On the basis of a better understanding of *Sanguinolites* and the assignment of species hitherto placed in *Sanguinolites* to *Myofossa, Pleurophorella* and *Gilbertsonia*, a more satisfactory definition of *Sanguinolites* is possible. The family contains more or less transversely elongate shells with a lunule and a distinct, flattish escutcheon. The ligament is lodged in an opisthodetic groove at the front point of the escutcheon, with a small slender nymph. Earlier, Dickins (1963) considered that the flattish elongated area (escutcheon) behind the umbones was a ligament area, but fresh work has shown that the bulk of the ligament, the spring part, is lodged in a groove at the front end of the area (Fig. 11d). It is possible, however, that the periostracal ligament was continuous with that covering the shell surface in this region and that it continued posteriorly to the distal end of the escutcheon (Yonge's (1957) fusion layer, see p. 54, discussion on hinges). Shells with granular surface spicules are found in this family. We divide the family into Subfamilies Sanguinolitinae, Undulomyinae, Pholadellinae, Alulinae, Chaenomyinae and Vacunellinae. The similarity of escutcheon and posterior area or corselet exhibited between the Sanguinolitidae and the permophorid *Pleurophorella*, which led Hind (1900) to include both in his interpretation of the genus *Sanguinolites*, has suggested to us a common origin for the two.

Subfamily **SANGUINOLITINAE** Miller, 1877

[*nom. trans.* herein, *ex* Sanguinolitidae Miller]

In this subfamily are placed the genera *Sanguinolites, Myofossa* and *Gilbertsonia* along with the several genera listed on p. 94. These forms were apparently adapted to a shallow infaunal environment. *Sanguinolites* especially retained unspecialized features. *Myofossa*, on the other hand, has characteristic features of the escutcheon which at some future time may serve as the basis for recognizing a separate subfamily. The family Permophoridae, to which *Sanguinolites* seems closely related, has specialized by the development of subumbonal hinge teeth for a shallow infaunal environment, and from time to time species became specialized for an endobyssate habitat.

Genus ***SANGUINOLITES*** M'Coy, 1844: 47

Type species. *S. discors* M'Coy (1844: 49; pl. 8, fig. 4), subsequently designated by Stolizcka (1871: xix, 270) (= *S. angustatus* (Phillips) (1836: 208; pl. 5, fig. 2)). Hind (1900: 367) concluded that M'Coy's type of *S. discors* was a young specimen of *S. angustatus* (Phillips, 1836), and our examination of the type specimens and other material confirms that *S. discors* is a junior subjective synonym of *S. angustatus* (Phillips) 1836.

Description. Elongate with umbones well anterior of midpoint. Well differentiated posterior dorsal area, with three radiating ribs present. The top one delimits an elongate marked escutcheon, there is a medially placed one, and a third, running to the posterior ventral margin, delimits the area itself and also the subvertical siphonal margin. The area is ornamented with comarginal growth laminae, some of which may form thin ribs. Ventral margin curved, flank ornamented with distinct rounded ribs separated by wider interspaces. Dorsal margin long and straight behind umbones set in a distinct escutcheon. A ligament groove extends behind the umbones, separating a slender but distinct nymph. The straight dorsal margins behind the nymph were probably joined by periostracal ligament (Fig. 6). Moderately impressed anterior adductor scar, rounded, with a deeply inset anterior pedal retractor at its dorsal umbonal edge extended more or less parallel to the anterior umbonal ridge, at about 45° to the cardinal margin and not at right angles as in the Permophoridae. No buttress visible.

Posterior adductor scar barely discerned. Pustules visible above ribs towards the anterior ventral margin in *S. costatus* Meek & Worthen 1869 (Upper Pennsylvanian, Texas). There are few records of pre-Carboniferous species of *Sanguinolites*, although we consider '*Leptodomus' acutirostris* Sandberger as illustrated by Beushausen (1895: pl. 24, figs 8–10) from the L. Devonian of the Rheinland to belong here or to a very closely related genus.

Sanguinolites angustatus (Phillips, 1836) Figs 5a–d

1836 *Sanguinolaria angustata* Phillips: 208; pl. 5, fig. 2.
1844 *Sanguinolites angustatus* (Phillips); M'Coy: 48.
1844 *Sanguinolites discors* M'Coy: 49; pl. 8, fig. 4.
1900 *Sanguinolites angustatus* (Phillips); Hind: 366–8; pl. 40, figs 1–6.
?1910 *Sanguinolites simulans* Girty: 224.
?1969 *Sanguinolites simulans* Girty; Pojeta: 16; pl. 3, figs 3–5.

Types. BM PL4272, the lectotype of *Sanguinolaria angustata* Phillips, from 'Bolland', Yorkshire/Lancashire border, Lower Carboniferous, Viséan. National Museum of Ireland, the lectotype (selected herein) of *Sanguinolites discors* M'Coy (1844: pl. 5, fig. 2). USNM 155895 is the holotype of *Sanguinolites simulans* Girty; Pojeta (1969: 16) stated that this is the only original specimen of Girty.

Other material. BM 97184 and BM L47471, 2 paralectotypes of *S. angustata* from Poolvash, Isle of Man. BM 52029 from Clifton, near Bristol. One paralectotype (Nat. Mus. Ireland, not numbered) of *Sanguinolites discors*, from the Arenaceous Shales at Bruckless, Dunkinelly, N.W. Ireland.

Remarks. We have examined and refigured (Fig. 5c) Phillips' type specimen of *Sanguinolaria? angustata* and M'Coy's type specimen of *Sanguinolites discors*. Our examination confirms the conclusion of Hind (1900: 366) that *S. discors* is a synonym of *S. angustatus*.

Sanguinolites costatus (Meek & Worthen, 1869) Fig. 6

1869 *Allorisma costata* Meek & Worthen: 171.
1873 *Allorisma costata* Meek & Worthen; Meek: 585–6; pl. 26, fig. 15.

Material examined. USNM 1506, two specimens from the Upper Carboniferous, Pennsylvanian Cisco Formation, near Jacksboro, Texas.

Remarks. This Upper Carboniferous species is very similar to *S. angustatus* in both shape and sculpture. It may be distinguished by its wider-spaced comarginal ribs. Small numbers

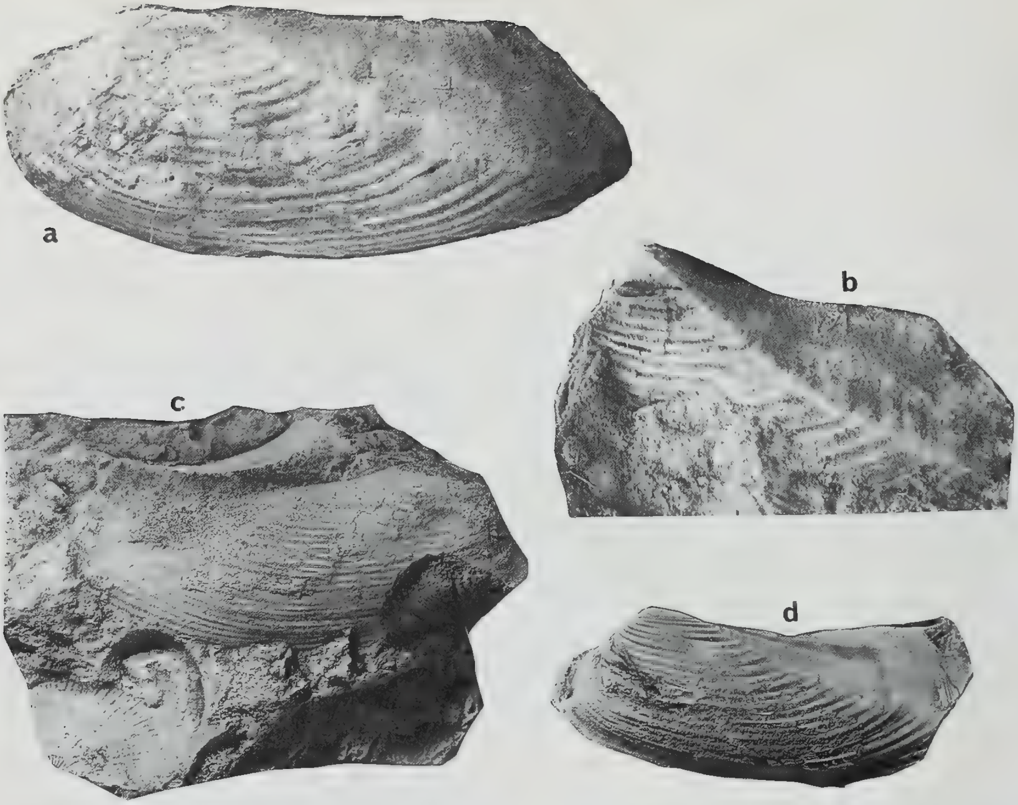


Fig. 5 *Sanguinolites angustatus* (Phillips). Figs 5a–b, Arenaceous shale, Bruckless, Dunkineely, County Donegal, Ireland: NMI, Griffiths Collection; Fig. 5a, **lectotype** (selected herein), and Fig. 5b, paralectotype (on same piece of rock), of *S. discors* M‘Coy, both ×3. Fig. 5c, Lower Carboniferous, Viséan, Bolland, Yorkshire; BM PL4272, Gilbertson Collection, lectotype of *Sanguinolites angustatus*, side view, ×1·5. Fig. 5d, Lower Carboniferous, Clifton, Bristol; BM 52029, ×1·3.

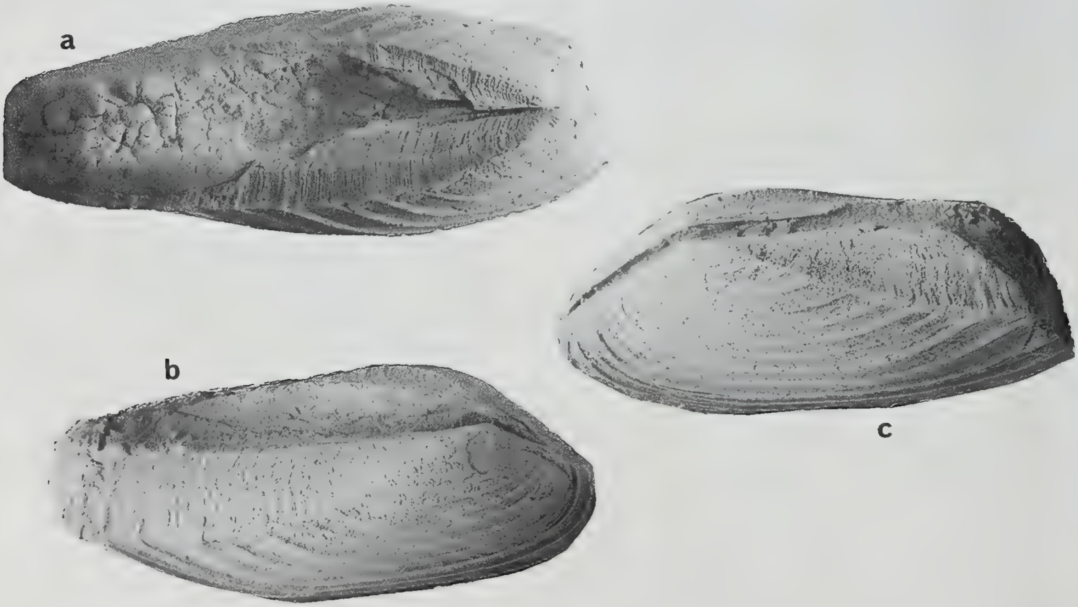


Fig. 6 *Sanguinolites costatus* Meek & Worthen. Locality *24827, Upper Carboniferous, Pennsylvanian, Cisco Formation, near Jacksboro, Texas; USNM Dr* 1506, Renfro Collection; Fig. 6a, top view; Fig. 6b, oblique dorsal view; Fig. 6c, slightly oblique view of left side showing the ligament nymph of the right valve; all approx. ×2.

of periostracal spicules were observed on the lower anterior part of the flank below the comarginal ribs. Our interpretation of this is that their function of maintaining the position of the shell in the sediment had been taken over by the comarginal ribs. The value of this species relates to its ligament attachment area being unequivocally well preserved. It has relatively long, low, slender nymphs separated from the outer escutcheon surface by a deep ligament groove.

*?**Sanguinolites argutus*** (Phillips, 1836) Figs 7a–b

1836 *Cucullaea arguta* Phillips: 210; pl. 5, fig. 20.
1897 *Cucullaea arguta* Phillips; Hind: 174.
1900 *Sanguinolites argutus* (Phillips) Hind: 368–9; pl. 40, figs 15–16.

HOLOTYPE. BM 97155, Lower Carboniferous, Viséan, 'Bolland', Yorkshire/Lancashire Border, England; Gilbertson Collection.

DISCUSSION. *?Sanguinolites argutus* is a much more tumid shell than *S. angustatus*. The posterior area or corselet is marked by a very sharp angularity, almost a carina; this leaves the area diverging from the plane of commissure at a fairly high angle until it approaches the siphonal margins. Hind described this species as one of the rarest in the Carboniferous. It may, however, prove to be an important species because it resembles *Myonia carinata* from the Permian of eastern Australia in its morphology. As yet we are uncertain whether this is due to convergence or whether it indicates a natural relationship.

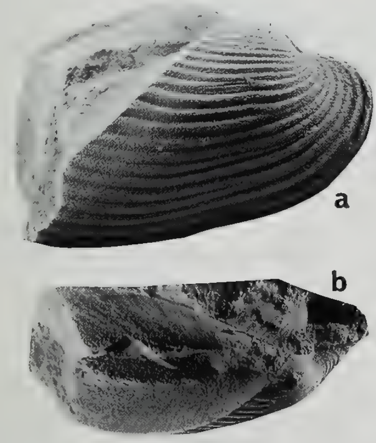


Fig. 7 *Sanguinolites argutus* (Phillips). Lower Carboniferous, Viséan, Bolland, Yorkshire, England; BM 97155, Gilbertson Collection, holotype; Fig. 7a, right side, Fig. 7b, dorsal view; both ×3.

Genus ***MYOFOSSA*** Waterhouse, 1969*b*

TYPE SPECIES. *Myonia subarbitrata* Dickins, 1963 (p. 48; pl. 5, figs 2–12) by original designation.

REMARKS. In attempting to decide on the correct generic name for this taxon we have considered the following nominal genera in addition to *Myofossa*:

Sedgwickia M'Coy, 1844, type species *S. attenuata* M'Coy, 1844, by subsequent designation of Stoliczka, 1871 (Fig. 8).

Palaeocorbula Cowper Reed, 1932, type species *P. difficilis* Cowper Reed, 1932, by monotypy (Fig. 15).

Grammysiopsis Chernychev, 1950, type species *Grammysiopsis irregularis* Chernychev, 1950, by original designation.

Ragozinia Muromzeva 1984; type species, *Ragozinia dembskajae* Muromzeva & Guskov *in* Muromzeva, 1984, by original designation.

DISCUSSION. The type specimen of *Sedgwickia attenuata* M'Coy (1844: 62; pl. 11, fig. 39; refigured by Hind, 1899: pl. 27, fig. 8) has been kindly lent by Dr Colm E. O'Riordan, formerly of the Natural History Division of the National Museum of Ireland, Dublin. It is refigured here (Fig. 8). *S. attenuata* is the type species of *Sedgwickia* by subsequent designation of Stoliczka (1871: xix, 271); Chernychev's (1950: 33) designation of *Sedgwickia gigantea* M'Coy is invalid. The generic name was used by Hind (1899) and Runnegar (1974: 932), and the species to which Runnegar refers are included here in *Myofossa*. However, Hind included a variety of species, including some that we would ascribe to the trigoniacean family Schizodidae. We are unable to interpret the type species, *S. attenuata*, from its holotype (Fig. 8), which is small and badly crushed. The ribbing is poorly preserved and there are no details of the hinge or musculature. In particular the characteristic form of the escutcheon which would allow us to refer it in the present genus is absent or not preserved. Recollecting from the type locality might show that M'Coy's species is a synonym of *Sanguinolites variabilis* M'Coy of Hind (not *Cosmomya variabilis* (M'Coy)). This species is described here as *Myofossa hindi* sp. nov. With the present state of knowledge the binomen *Sedgwickia attenuata* M'Coy, 1844 should be rejected as a *nomen dubium*.

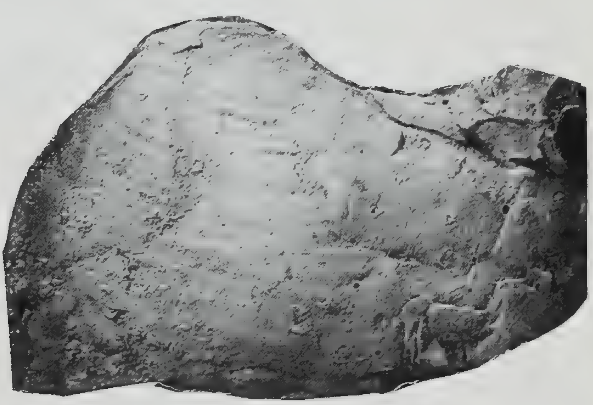


Fig. 8 *'Sedgwickia attenuata'* M'Coy (*nomen dubium*). Lower Viséan, Arenaceous Shale [of Yellow Sandstone Group], River Bannagh, Drumcurren (near Kesh, County Fermanagh), Northern Ireland; NMI, Griffiths Collection, holotype; view of crushed composite mould of left valve, ×3.

Chernychev (1950) included two species in his new genus *Grammysiopsis:* the type species, *G. difficilis*, and *G. kazachstanensis* n. sp. His own *'Grammysioidea' welleroides* (Cherychev, 1950: pl. 7, fig. 68 only) may be a synonym of the latter. His type species is rather poorly illustrated and we were unable to say with certainty whether this is a *Myofossa*. The peculiar grouping and turning of the comarginal ribs towards the posterior area suggest to us that this should be considered as a separate genus, at present not described outside the USSR. However, the second species, *G. kazachstanensis* (Cherychev, 1950: pl. 6, figs 53a–d, 54a–b) is almost identical to *Myofossa hindi* described here. Other species doubtfully included by Chernychev, *G. donaica* and *G. obscura*, may be synonyms of *Cosmomya variabilis* (M'Coy). The problem appears to have been solved by Muromzeva (1974), who illustrated a number of species of *Grammysiopsis*, ranging from the Viséan to the Carboniferous–Permian boundary, that have the same characteristic twist to the ribs as Chernychev's type species. From this material from Kazakhstan and the Soviet Arctic we can see that *Grammysiopsis* may be easily distinguished from *Myofossa* by the enormous size of its posterior gape. *Grammysiopsis* appears to be a distinct offshoot of *Myofossa* which has developed much more substantial siphons, presumably of type 'C', that has so far not been recognized outside the Soviet Union.

Cowper Reed's (1932) genus *Palaeocorbula* is based on a single specimen (Figs 14a–c). It is smaller than most species of *Myofossa* and shows no sign of the posterior attenuation. This marked difference in shape leads us to accept it as a distinct genus. It is possible, however, that the specimen is deformed and the similar pattern of ribbing on the anterior and central part of the flank may necessitate the future synonymizing of the two taxa when more material becomes available.

SUBDIVISIONS OF *Myofossa*. At present we recognize two subgenera of *Myofossa: Myofossa* s. str. and *Ragozinia*. Species of *Myofossa* from the British Lower Carboniferous have been described as *Sanguinolites* by Hind (1900). All species of *Myofossa* are more convex, relatively shorter and do not have the distinctly delimited and sculptured corselet possessed by *Sanguinolites*. Driscoll (1965) included the species *Myofossa omaliana* (de Koninck), which occurs in both NW Europe and the U.S.A., in *Grammysia*. However, the latter genus has a less attenuate posterior shell, a less well defined siphonal area, usually no gape and a completely simple pallial line.

DIAGNOSIS. Oval in shape. Distinguished mainly by the features of the escutcheon. This consists of an internal heart-shaped area in which the ligament is lodged in a groove immediately below the umbo; in turn this is bound externally by a distinctly marked-off escutcheon which is again bounded externally by the umbonal ridge. Shell generally gaping at the rear with a more or less well developed sulcus running from the umbo towards the mid-part of the ventral margin. Flank usually bearing distinct, low, comarginal ribs, often fewer in number in a distinct anterior area, and more on the main part of the flank.

REMARKS. A number of Carboniferous species share the characteristic features of *Myofossa*. The Carboniferous species have a small ligament nymph, but this hardly seems sufficient to place them in a different genus. They include *Sanguinolites omalianus* de Koninck, 1842, *S. costellatus* M'Coy, 1851*a*, and *Myofossa hindi*, which can be distinguished from *Sanguinolites* proper, as well as some other genera, by their more oval shape. From other Megadesmidae and Edmondiidae they are distinguished by the distinctive features of their escutcheon.

During the course of this work we first thought that *Myofossa* might be placed with the Megadesmidae. However, the nature of the escutcheon and the persistence of this feature in bivalves from the middle of the Palaeozoic to the Mesozoic has caused us to regard this feature as of considerable importance. We have, therefore, assigned *Myofossa* to the Sanguinolitidae which have similar characteristics of the escutcheon.

Species of *Myofossa* have a variety of shell form comparable with living species of *Laternula* Röding, 1798. At present it does not seem to us that the earlier species of the Laternulidae and the Thraciacea as a whole are derived from them; we consider it more likely that the similarity between Upper Palaeozoic *Myofossa* and Recent Laternulidae is a matter of partial convergence.

Subgenus ***MYOFOSSA* (*MYOFOSSA*)**

Myofossa (Myofossa) subarbitrata (Dickins, 1963) Figs 9a–f

1963 *Myonia subarbitrata* Dickins: 48–9; pl. 5, figs 2–12, 22.
1969*b* *Myofossa subarbitrata* (Dickins) Waterhouse: 32, 66.

MATERIAL. The type material from the Lower Permian, Nura Nura Member of the Poole Sandstone Formation, of the Canning Basin, Western Australia, all in the Bureau of Mineral Resources and Mines, Canberra, Australia.

DISCUSSION. New illustrations are given here (Figs 9a–f) to show the striking similarity between the present species and British Carboniferous species of *Myofossa*.

Myofossa (Myofossa) hindi sp. nov. Figs 10a–e

1851*a* *Sanguinolites variabilis* M'Coy: 174 (pars).
1855 *Sanguinolites variabilis* M'Coy; M'Coy: 508; pl. 3f, fig. 7 only.
1900 *Sanguinolites variabilis* M'Coy; Hind: 379; pl. 44, figs 3–8 only.
?1900 *Sanguinolites variabilis* M'Coy; Hind: 379; pl. 44, fig. 1 only.
?1900 *Sanguinolites v-scriptus* Hind: 382; pl. 42, figs 5, 5a only.

HOLOTYPE. BM L47511, from the Viséan Redesdale Ironstone (Figs 10a–d) (also figured by Hind, 1900: pl. 44, fig. 3.)

PARATYPES. BM L47512–47516, the specimens figured by Hind (1900: pl. 44, figs 4, 4a, 5, 6, 7 & 8) and BM L3231 (Fig. 10e here), all from the Redesdale Ironstone; Sedgwick Museum, Cambridge, the type of M'Coy's ovate variety of *Sanguinolites variabilis*, from the Carboniferous Limestone of Lowick, Northumberland.

DIAGNOSIS. Broadest towards front part of shell, fairly evenly rounded from front to back, not tumid. Umbones not especially raised above dorsal part of shell. Carina rounded. Rapid increase in number of ribs towards the rear along line of greatest tumidity.

DESCRIPTION. Features of the genus are well shown in the material from the Redesdale Ironstone. The lunule and the escutcheon are distinct. A groove is present on either side of the carina outside of which there is an area between the groove and the rounded carina which has ribs less well developed than in front of the carina. The posterior has a

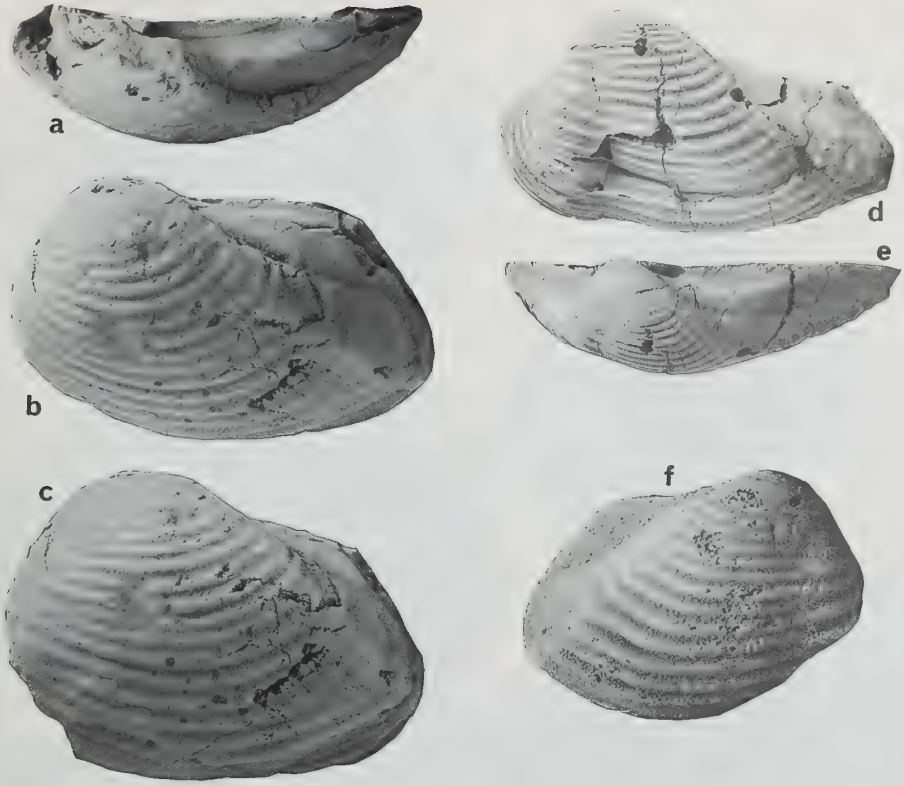


Fig. 9 *Myofossa (Myofossa) subarbitrata* (Dickins). Lower Permian, Nura Nura Member of Poole Sandstone Formation, 1·6 miles SW of Paradise Homestead, Canning Basin, Western Australia. Figs 9a–c, BMR CPC 3885, holotype; Fig. 9a, top view; Fig. 9b, oblique view showing siphonal area; Fig. 9c, view of left side; all ×3. Figs 9d–e, BMR CPC 3886, paratype A; Fig. 9d, view of left valve; Fig. 9e, top view; both ×2. Fig. 9f, BMR CPC 3887, paratype B, side view showing slight subumbonal sulcus, ×3.

significant gape. A narrow ligament groove is shown behind the umbo in BM L47314 and the hinge appears to be edentulous. The ribbing is distinctive. In the holotype, 16 ribs can be counted in the front part of the shell which are more or less concentric. The rib number increases rapidly by interpolation and 39 are present in the most tumid part of the shell; some of the added ribs make a distinct Y-like bifurcation with ribs at the front. A rounded posterior adductor muscle scar is shown in BM L3231 and the back part of the pallial line has a shallow sinus.

BM L47515, from Redesdale, has a well-preserved short nymph with a narrow, lunate ligament groove separating it from the escutcheon. Its inner surface is juxtaposed to the other nymph and does not project inwards from the remaining part of the posterior dorsal shell margin.

Remarks. Hind (1900: 381) recognized that M'Coy (1851*a*: 174; 1855: 508; pl. 3f, figs 6, 6a, 7, 7a) had included two distinct shells in *Sanguinolites variabilis*. Elsewhere (p. 69) we have pointed out that the specimen in M'Coy, 1855: pl. 3f, fig. 6, 6a, is the lectotype of *Cosmomya variabilis* (M'Coy), selected by Hind (1900), and a new name is now required for the other specimen. Driscoll (1965: 91) included this species as a synonym of *Myofossa [Grammysia] omaliana* (de Koninck) in his redescription of that species. However, although *Myofossa hindi* has a similar shape to *M. omaliana*, the ornament, particularly the density and style of splitting of the ribs, is quite distinctive. Both species occur in the British Isles, but in rather different lithologies and apparently never together. *M. hindi* is known only from the Carboniferous Limestone at Lowick and from the shell band in the Redesdale Ironstone, D_2 Zone, both in Northumberland. *M. omaliana*, on the other hand, occurs in Viséan limestone in Kildare and Limerick, commonly at Thorpe Cloud, Derbyshire, and in the lowest Namurian Great Limestone at Stanhope, Northumberland.

Myofossa (Myofossa) omaliana (de Koninck, 1842)

Figs 11a–d

1842 *Pholadomia omaliana* de Koninck: 65; pl. 5, fig. 4a–b.
1885 *Chaenomya omaliana* (de Koninck); de Koninck: 6; pl. 1, figs 12–15.
1900 *Sanguinolites omalianus* (de Koninck); Hind: 372–4; pl. 40, figs 17–24.

Type material. Not seen, lent to de Koninck by M. Puys, from 'l'argile de Tournay', Tournaisian, Belgium.

Remarks. This seems to be a very widespread species, occurring throughout the Lower Carboniferous and the base of the Upper Carboniferous, in Belgium, the British Isles and the United States. It has been extensively discussed by Driscoll (1965), but does not include *Sanguinolites variabilis* M'Coy, *pars (=Myofossa hindi* sp. nov.), see above.

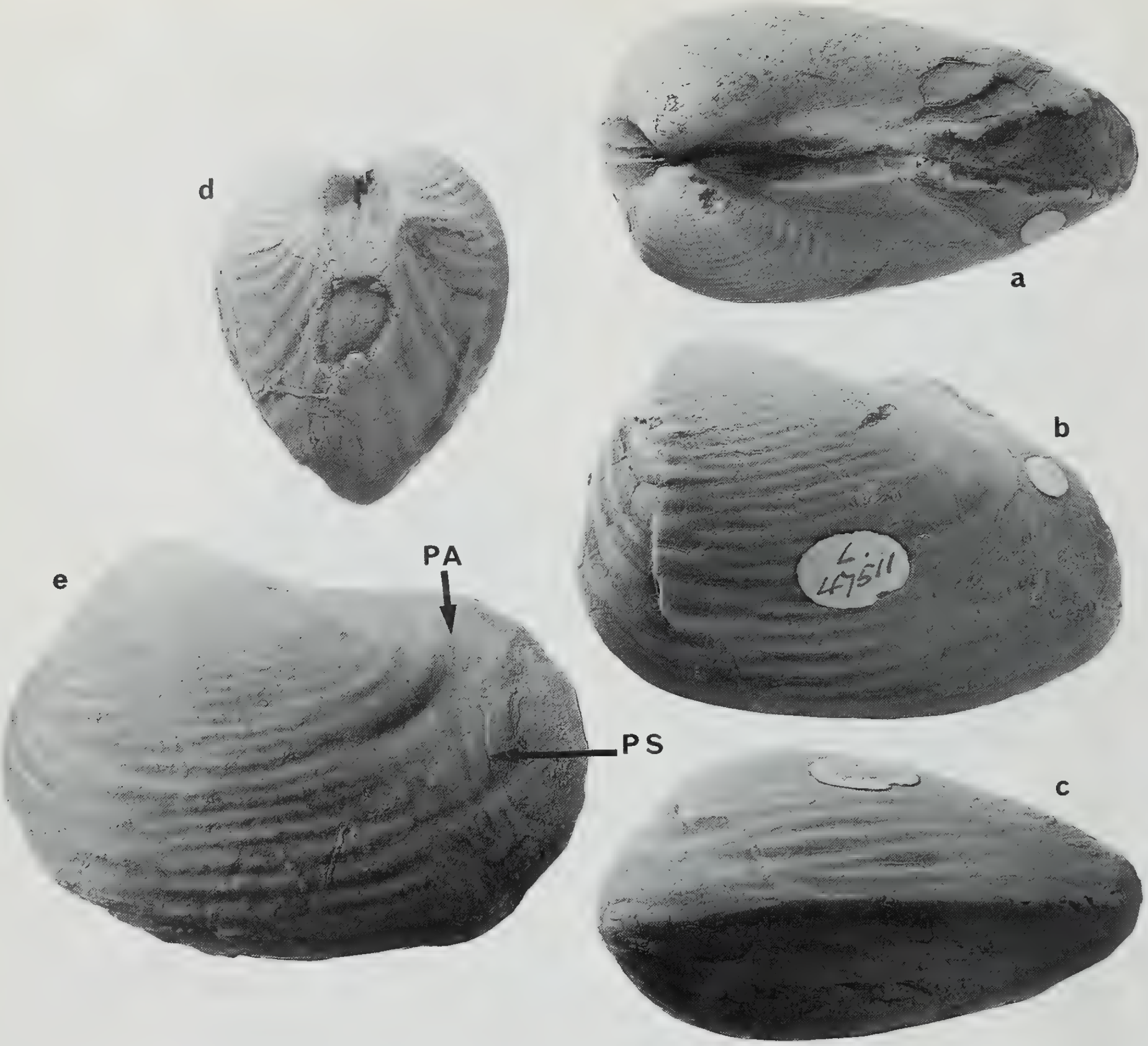


Fig. 10 *Myofossa hindi* sp. nov. Lower Carboniferous, Viséan, Asbian, Redesdale Ironstone, Redesdale, Northumberland. Figs 10a–d, BM L47511, holotype, bivalved specimen (Hind, 1900: pl. 44, fig. 3); Fig. 10a, dorsal view; Fig. 10b, view of left side; Fig. 10c, ventral view; Fig. 10d, anterior view. Fig. 10e, BM L3231, paratype, view of left valve of steinkern; PA — posterior adductor, PS — pallial sinus. All ×2.

Myofossa (Myofossa) costellata (M'Coy, 1851)
Figs 1, 12a–d

1851*a* *Leptodomus costellatus* M'Coy: 174.
1855 *Leptodomus costellatus* M'Coy; M'Coy: 508; pl. 3f, fig. 5.
1900 *Sanguinolites costellatus* M'Coy; Hind: 377–9; pl. 41, figs 8–10.

Syntypes. SM E13273 (M'Coy, 1855: pl. 3f, fig. 5), and four unfigured syntypes, SM E9319–22, all from the Lower Limestone Series (Viséan) of Craige, Kilmarnock, Ayrshire, Scotland.

Remarks on nomenclature. *Myofossa costellata* is a junior secondary homonym of *Sanguinolites costellatus* M'Coy, 1844, considered by Hind (1900: 379) to be the posterior end of an internal cast of *Solemya costellata*.

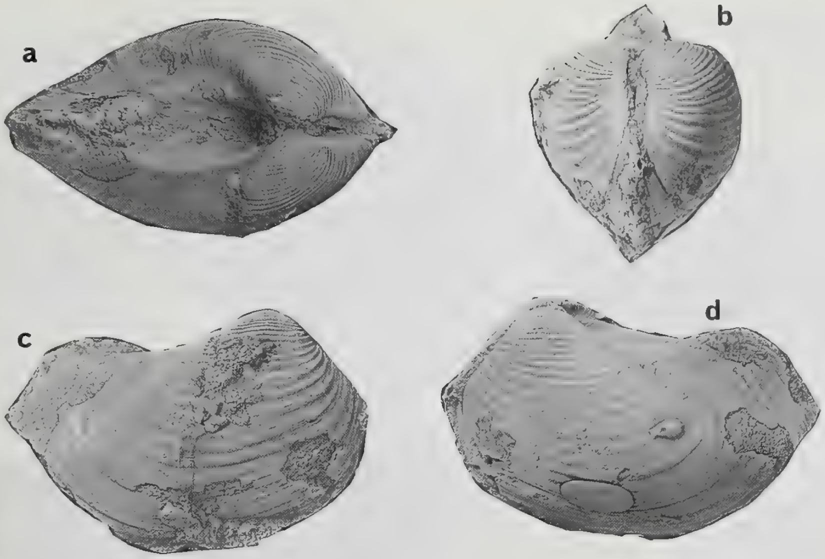
Discussion. *Myofossa costellata* is evenly ribbed, and has 50% more ribs per unit distance from the umbones than *M. hindi*. Like *M. hindi*, it also occurs in very fine-grained facies. It is more elongate than the other species described here. It has not been found to occur with either *M. omaliana* or *M. hindi*. The fine ribbing recalls that of *Ragozinia*, but it dies not have the smoother sub-umbonal part of the flank.

Subgenus ***RAGOZINIA*** Muromzeva, 1984

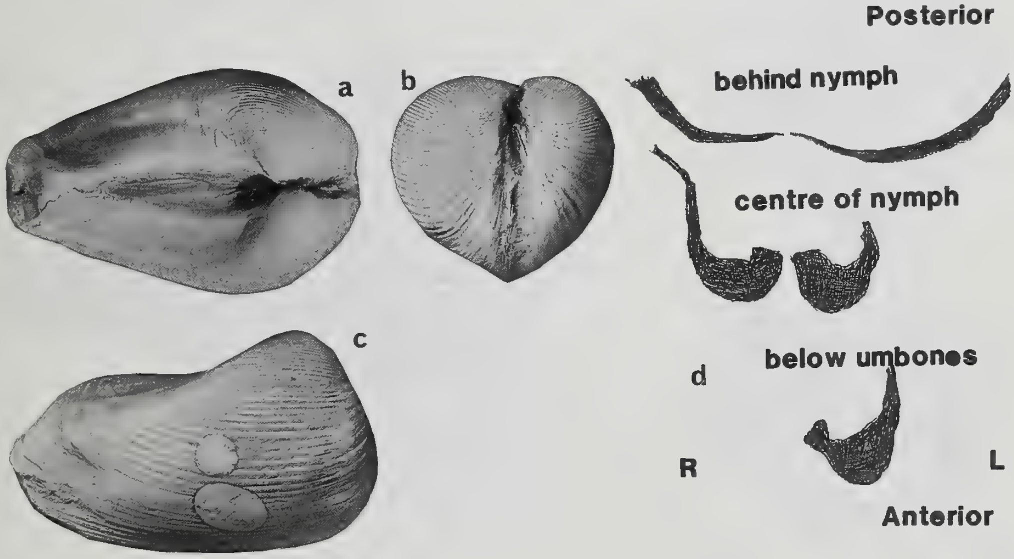
Type species. *Myofossa (Ragozinia) dembskajae* (Muromzeva & Guskov, *in* Muromzeva 1984) (? = *Myofossa (Ragozinia) amatopensis* (Thomas, 1928)).

Myofossa (Ragozinia) amatopensis (Thomas, 1928)
Figs 13a–e

1928 ?*Sanguinolites amatopensis* Thomas: 224–5; pl. 6, figs 10, 10a.
1963 *Chaenomya* sp. Dickins: 51; pl. 8, figs 12–16.



ig. 11 *Myofossa omaliana* (de Koninck). Lower Carboniferous, Kildare, Ireland; BM 26327; Fig. 11a, top view; Fig. 11b, anterior view; Fig. 11c, view of right side; Fig. 11d, view of left side. All ×1.



ig. 12 *Myofossa costellata* (M'Coy). Lower Limestone Shale, Lower Carboniferous, Gurdy railway cutting, Gurdy, near Beith, Ayrshire, Scotland; BM L47489; Fig. 12a, top view; Fig. 12b, anterior view; Fig. 12c, view of right side; all ×1·25. Fig. 12d, BM L46425, transverse sections through ligament nymph, with detached nymph of right valve re-orientated to original position; approx. ×13; see also Fig. 1.

?1976 *Myonia (Myonia) gorskyi* Astafieva-Urbaitis: 32; pl. 3, fig. 5.

f. 1984 *Ragozinia gorskyi* (Astafieva-Urbaitis); Muromzeva: 113–14; pl. 41, figs 6–8.

?1984 *Ragozinia dembskajae* Muromzeva & Guskov, *in* Muromzeva: 114; pl. 41. figs 2, 4, 5.

OLOTYPE. SM A4971, from the 'Goniatite Bed', Parinas uebrada, Peru, Permian (not Upper Carboniferous as in-erpreted by Thomas); Barrington-Brown collection. The ype material of this species was apparently mistakenly ssociated with Pennsylvanian ammonoids when collected.

THER MATERIAL. BM L9448, Irwin District, Perth Basin, estern Australia, no horizon recorded, but almost certainly Fossil Cliff Formation, Late Sakmarian; University of Western Australia, type no. 45374 (Dickins 1963: pl. 8, figs 12–13), from the Fossil Cliff Formation, Fossil Cliff, Perth Basin; Commonwealth Palaeontological Collection (C.P.C.) No. 3881, from the Callytharra Formation, Carnarvon Basin; C.P.C. No. 3882, from the Nura Nura Member of the Canning Basin. These are all thought to be of Lower Permian, Late Sakmarian age.

DIMENSIONS. BM L9498: length 84mm, height 48mm, width (two valves) 35mm, gape *c*. 9mm.

DISCUSSION. During reorganization of the collections at the British Museum (Natural History) BM L9498 was found with Mesozoic specimens. It was recognized as specifically identical

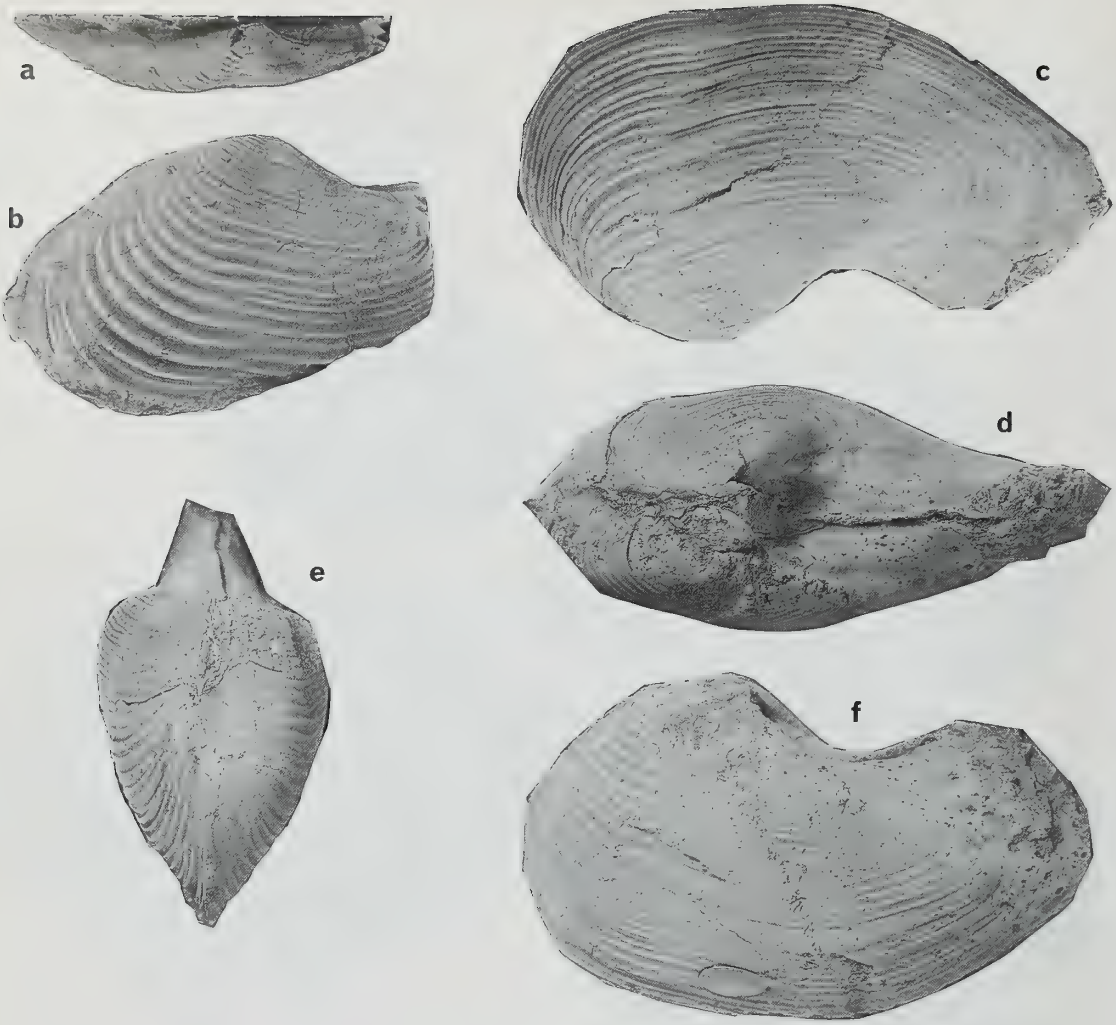


Fig. 13 *Myofossa (Ragozinia) amatopensis* (Thomas). Figs 13a–b, Permian, 'Goniatite' bed, Parinas Quebrada, Amatope Mountains, northwest Peru; SM A4971, Barrington Brown Collection, holotype; Fig. 13a, top view; Fig. 13b, left side. Figs 13c–f, Lower Permian, Sakmarian, Fossil Cliff Formation, Irwin District, Western Australia; BM L9498; Fig. 13c, right side; Fig. 13d, top view; Fig. 13e, anterior view; Fig. 13f, left side. All ×1.

with the specimens described by Dickins and there is now adequate material to indicate that this is a very widespread species. The matrix of the newly discovered Australian specimen, BM L9498, is that of the Fossil Cliff Formation. The label with the specimen reads 'Irwin District, Western Australia. Presented H. P. Woodward, May 1892'. The specimen apparently came from Fossil Cliff.

Although Runnegar (1969: 285) has suggested this species belongs to *Australomya*, the features of the escutcheon show that it belongs to *Myofossa*. When we compared the Australian material with Thomas' Peruvian holotype we were unable to find any significant differences. The Western Australian specimens and the holotype show considerable similarity to the Carboniferous species assigned in this paper to *Myofossa*, and especially to *S. (Ragozinia) gorskyi* from the Kungurian of the USSR, though the specimens from Western Australia are rather larger. Muromzeva (1984) distinguished a separate species, *M. (R). dembskajae*, which had a much more attenuated posterior. We have not been able to examine any of her material, but we suspect the differences may be due to crushing. The posterior part of the shell, however, is more upturned in *M. (R.) amatopensis* than in the Carboniferous species, probably reflecting adaptation to deeper burrowing. *M. (R.) amatopensis* differs from its contemporary, *M. subarbitrata*, in lacking a concave anterior margin, its much finer ribbing and in being upturned at the back.

Myofossa sp. subgenus undetermined Fig. 14

MATERIAL. USNM Ass 161469, Graham (top of Jacksboro), Old Gunter Road, 0.5 miles south of Texas 24, 5 miles NE of Jacksboro, Texas. USNM DR II 1506, Renfro Collection, loc. 1506, similar horizon, Upper Pennsylvanian, Texas.

DESCRIPTION. This apparently undescribed species has sculpture of the same general pattern as *Myofossa*, s. str., but much more exaggerated. There is an anterior field of prominent comarginal ribs with obvious radiating pustulose striae.

These striae are more randomly arranged within the ill-defined lunule, which is terminated at the sub-umbonal sulcus where it meets the ventral margin anterior to the umbones at a distinct sinus in the shell margins. The larger, main area of the flank is an area of low comarginal ribs and radial striae. These pustulose radial striae stop abruptly at the posterior area, which has strong transverse ridges parallel to the siphonal margins. There is no carina to the escutcheon which has periostracal creases on the shell surface and an ill-defined lunule.

REMARKS. *Myofossa* sp. has a wider central field of comarginal ribs, extending well anterior to the umbones, than ?*Grammysiopsis maria* (Worthen; Runnegar 1974: pl. 3, figs 1, 2, 11). The species may eventually prove to belong to *Grammysiopsis*.

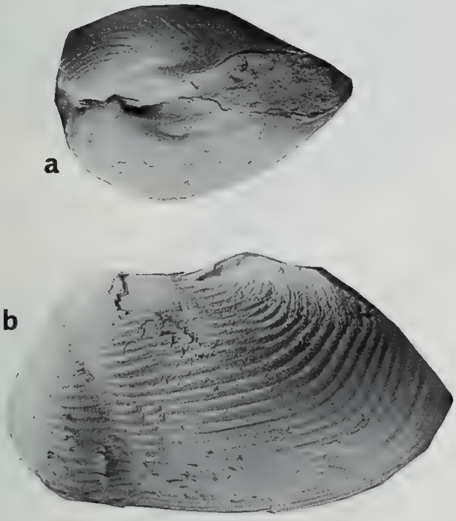


Fig. 14 *Myofossa* sp. nov. Upper Pennsylvanian, Graham Formation (top of Jacksboro Member), Old Gunter Road, 0·5 mile south of Texas 24, 5 miles NE of Jacksboro, Texas; USNM Ass 161469; Fig. 14a, top view, with posterior end tilted upwards; Fig. 14b, left side; both ×1·7.

Genus ***PALAEOCORBULA*** Cowper Reed, 1932
Figs 15a–c

TYPE SPECIES. *Palaeocorbula difficilis* (Cowper Reed, 1932), by monotypy.

DISCUSSION. There are strong similarities between the shape and sculpture of *Myofossa* and *Palaeocorbula*. This latter genus is based on a single specimen of *P. difficilis* from Middle Horizon One, of the Lower Permian Agglomerate Slates of Kashmir. The specimen is housed in the collections of the Geological Survey of India, Calcutta; we have been kindly supplied with photographs of the type by S. C. Shah, Director of Palaeontology and Stratigraphy at the Geological Survey of India, which are reproduced here (Fig. 15). In our interpretation the short, coarse comarginal ribs are anterior and they bifurcate at a short distance from the anterior margin, in a similar manner to most other species of *Myofossa*. The posterior siphonal area is nearly smooth. In the holotype the valves are mutually displaced and much of the corselet of the two valves is apparently missing (Fig. 15). It appears to us that the posterior of the left valve has been somewhat foreshortened by diagenetic or tectonic deformation. These vagaries of preservation apparently led Cowper Reed to interpret the animal as inequivalve and place the genus in the Corbulidae. It is the strong similarity in style of ribbing between *Palaeocorbula* and *Myofossa subarbitrata* (Fig. 9), and a number of other species belonging to the genus, that allows us to interpret *Palaeocorbula* as a close relative of *Myofossa*.

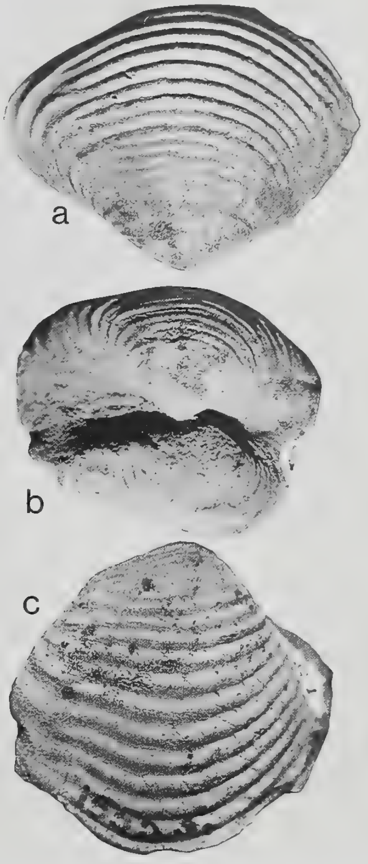


Fig. 15 *Palaeocorbula difficilis* (Cowper Reed). Upper Permian, Kashmir, India; GSI 15553, holotype; Fig. 15a, right side; Fig. 15b, top view; Fig. 15c, left side; all ×1·5.

Genus ***COSMOMYA*** Holdhaus, 1913

TYPE SPECIES. *Cosmomya egraria* Holdhaus (1913: 446; pl. 94, fig. 3a–c), by monotypy. A plaster cast of the type specimen in the GSI has been figured by Dickins & Shah (1965: pl. 17, fig. 13–14).

SYNONYMY. *Palaeocosmomya* Fletcher, 1946 (type species, *P. teicherti* Fletcher, 1946 by original designation (?=*Cosmomya egraria* Holdhaus, 1913; ? = *Cosmomya artiensis* (Krotova, 1885: 255; pl. 3, fig. 20)).

DISCUSSION. The relationship between *Cosmomya* and *Palaeocosmomya* has been discussed by Dickins & Shah (1965). At that time the family relationships of the genus were obscure but the early species from the British Lower

Carboniferous, particularly the material in the British Museum (Natural History) described by Hind (1900) as *Sanguinolites v-scriptus*, show a transition between early species of *Myofossa* to *Cosmomya* by the gradual acquisition of typical eccentric zig-zagging ribs. This has led us to place *Cosmomya* in the Sanguinolitidae. *Cosmomya* differs from *Grammysiopsis* Chernychev, 1950 and *Pentagrammysia* Chernychev, 1950 by the position of these ribs, and it differs from *Praeundulomya* Dickins, 1957, by the shell shape and by lacking the posterior elongate shell thickenings that run close to the hinge in that genus. *Pentagrammysia*, a genus that has developed the ribbing style of the Mesozoic genus *Goniomya* independently, seems to have evolved in central or eastern Asia separately from *Cosmomya*, but we suggest that it also has common ancestry with a species of *Myofossa*. Several species of *Pentagrammysia* are illustrated in Muromzeva's publications (particularly 1974: pls 21–23). In the British species described below, ascending stratigraphical position reflects increasing complexity of ribbing pattern. Early species of the Mesozoic genus *Goniomya* differ from the type species of *Cosmomya, Pentagrammysia* and *Siphogrammysia* in having a sub-umbonal V in the ribbing which slopes downwards and backwards, and is horizontally truncated at least in the umbonal area. We have not been able to decide whether *Goniomya* is directly descended from one of these Upper Palaeozoic genera with V ribbing, or whether *Goniomya* has developed this style of ribbing independently. The material figured by Runnegar (1974: pl. 3, figs 1, 2, 11) as *Cosmomya maria* (Worthen) is better placed in *Grammysiopsis*, and if both fragments do in fact belong to the same species, they do not differ significantly from *G. bisulcatiformis* Muromzeva & Kagarmanov (*in* Muromzeva 1974: 108; pl. 23, figs 21–22).

Cosmomya v-scripta (Hind, 1900) Figs 16a–b

1900 *Sanguinolites v-scriptus* Hind: 382; pl. 42, figs 6, 6a, 7, 7a only.

Lectotype. BM L47495 (BM L46533 is the counterpart), here designated, is Hind's (1900: pl. 42, figs 7, 7a) figured specimen; it is from a marine sand approximately 500ft. below the third bed of Millstone Grit, probably E2 Zone, Congleton Edge, Cheshire, England. Fig. 16.

Paralectotypes. BM L47494, the specimen figured by Hind (1900: pl. 42, figs 6, 6a), the same horizon and locality as the lectotype. The second paralectotype, BM L47493 also figured by Hind (1900: pl. 42, figs 5, 5a), should be referred to *Myofossa hindi*; it is from the Redesdale Ironstone. We have found no other material.

Diagnosis. Escutcheon and groove inside rounded posterior carina developed as in *Myofossa*. Posterior V of ribbing distinct, but only a slight anterior V. A slight sulcus runs from the umbo to the anterior part of the dorsal margin in the position of the slight anterior V of the ribbing.

Description. Little can be added to Hind's description and to the diagnosis. The three specimens are deformed in different directions, and measurements are not meaningful. The lectotype is compressed laterally, and the paralectotype BM L47494 is elongated front to back. Despite this the principal characteristics of the species seem clear enough. The prominent umbo of BM L47493 from the Redesdale Ironstone is apparently an artefact, and although this specimen is quite small, it is clearly a different species.

Discussion. The relationship of this species to *Myofossa* on the one hand and to the type species of *Cosmomya* on the other hand seems well established. The characters associated with the escutcheon are essentially those of *Myofossa*. The anterior sulcus and ribbing represent the basic pattern of *Cosmomya*. The anterior V in the ribbing, however, is only slightly developed and the posterior V is less distinct. The pattern, however, is so close that there is little doubt that *Cosmomya v-scripta* is an ancestral species of the genus.

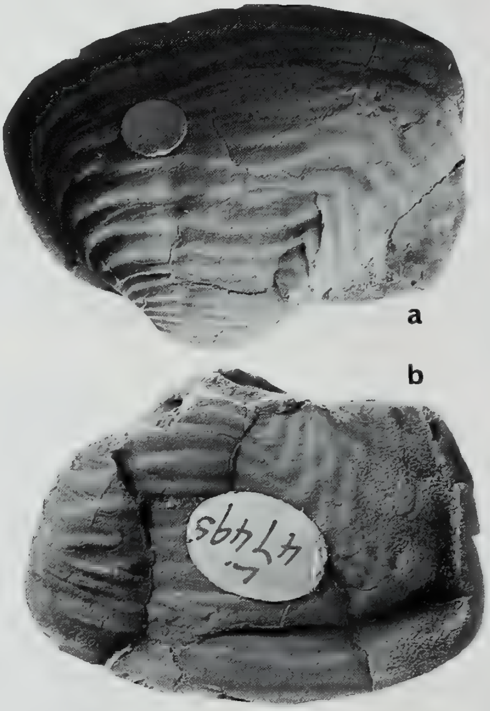


Fig. 16 *Cosmomya v-scripta* (Hind). Namurian (probably E2), marine sand *c.* 500 ft below third Millstone Grit, Congleton Edge, Cheshire; BM L47495, **lectotype** (selected herein); Fig. 16a, right valve; Fig. 16b, left valve; both ×2·5.

C. v-scripta resembles *'Grammysiopsis' omolonicus* Muromzeva (1974: 108; pl. 21, figs 1–3), which comes from near the Permo-Carboniferous boundary in the Omolonsk Massif, Irbichan, U.S.S.R. It does not, however, have such an extensive posterior gape and area. '*G.*' *bisulcatiformis* Muromzeva & Kazamanov (*in* Muromzeva 1974: 108; pl. 22, fig. 21) is difficult to distinguish from '*G.*' *omolonicus*; both species differ in having a considerably deeper V in the ribbing.

Cosmomya variabilis (M'Coy, 1851) Figs 17a–d

1851*a* *Sanguinolites variabilis* M'Coy: 174, *pars*.
1854 *Sanguinolites variabilis* Morris: 223.
1855 *Sanguinolites variabilis* M'Coy: 508; pl. 3f, figs 6, 6a only.
1900 *Allorisma variabilis* (M'Coy); Hind: 424; pl. 44, fig. 2.
1900 *Sanguinolites interruptus* Hind: 383; pl. 42, figs 8, 9, 10; pl. 49, fig. 10.

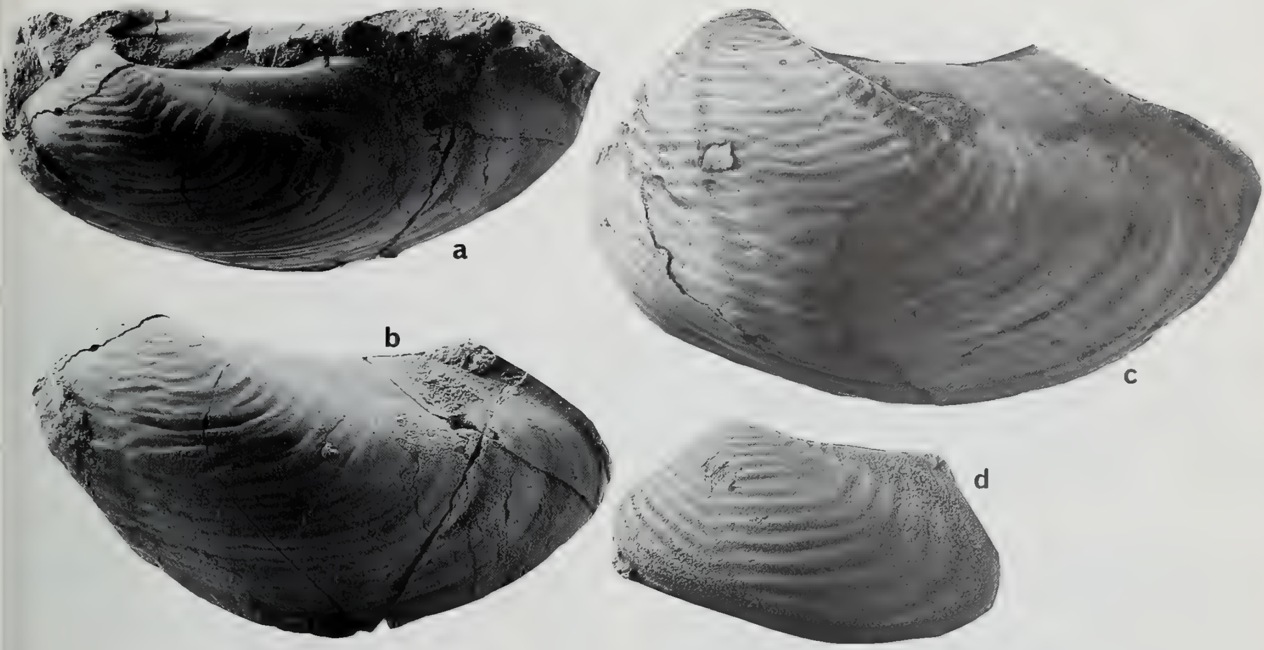


Fig. 17 *Cosmomya variabilis* (M'Coy). Figs 17a–b, High Viséan, Lowick, Northumberland; SM E1100, lectotype; Fig. 17a, angled top view; Fig. 17b, side view (note that the anterior ventral part of the shell is missing). Fig. 17c, Lowest Namurian, Main Limestone, Stanhope, Weardale, Northumberland; BM PL1598, left valve. Fig. 17d, Lower Carboniferous, Viséan, Thorpe Cloud; BM L47497, syntype of *Sanguinolites interruptus* Hind, left side. All ×1·5.

LECTOTYPE. SM E1100 (M'Coy, 1855: pl. 3f, figs 6, 6a), ubsequently designated by Hind (1900: description of pl. 44, ig. 2).

SYNTYPES OF *Sanguinolites interruptus*. These are BM L47496 (Hind, 1900: pl. 42, fig. 8), BM L47497 (Hind, 1900: pl. 42, ig. 10), BM L47538 (Hind, 1900: pl. 49, fig. 10), and one specimen from the same locality said by Hind to be in the collection of Mr Holroyd of Manchester; all are from the Lower Carboniferous, Viséan of Thorpe Cloud, Derbyshire, England.

OTHER MATERIAL. BM L46434–40, 7 specimens from Castleton or Thorpe Cloud in the Hind Collection; BM L43637, from Narrowdale, and BM L46433 from Gateham, between Wetton Hall and Narrowdale; all Lower Carboniferous, Viséan.

DESCRIPTION. Oval, tumid shell with distinct rugae, which are traight or slightly curved and comarginal in the mid part of he flank, but diverge across the growth lines in the anterior part forming a slight V. There is an indistinct V in the posterior part before they curve round with the siphonal margin. The greatest tumidity is posterior to the umbones. Umbo moderately distinct, pointed towards the front. The lunule is obscure and the escutcheon is typical for *Cosmomya* nd *Myofossa*. There is a rounded carina ventrally, and above his a groove running to the posterior margin of the posterior lattened area; above this the escutcheon proper is an elongated flat area bordering the external margin of the shell. From comparison with similar shells, a ligament groove and nymph might be expected at the anterior part of this flat area. A slight posterior gape was probably present. A shallow sulcus runs from the umbo to the ventral margin.

DIMENSIONS (mm):	Length	Height	Width
BM L47497, LV	39	23	9
BM L47496, LV	31	19	8

DISCUSSION. Two distinct species are represented in M'Coy's (1855) illustrations: i.e. his pl. 3f, figs 6 and 6a, and his pl. 3f, figs 7 and 7a. The identity of his third specimen (pl. 3f, fig. 8) is not clear, but it may be the same as his pl. 3f, figs 6 and 6a, as suggested by M'Coy himself when he described it as an oblong variety.

Hind (1900: 381) recognized these two different species and he referred them to two genera, *Sanguinolites* and *Allorisma*, both with the specific name *variabilis* attributed to M'Coy. Hind's choice of lectotype is in accordance with I.C.Z.N. Article 74 (a) (v), which states that a specimen that was not originally described as a syntype, i.e. was described as a variety, is not available for choice as lectotype. He incorrectly determined the specimen as an *Allorisma* (*Wilkingia* in terms of present usage), apparently failing to notice the incipient Vs of the discordant ribbing present on the lectotype; he included specimens of *Wilkingia regularis* de Verneuil in the same species. The lectotype, although damaged in the anterior region, is clearly the same species as BM PL1598, from the Lower Namurian Main Limestone of Stanhope near Durham, see Fig. 17c.

The V in the ribbing of this species is the only apparent difference from the genus *Myofossa*, but we consider this sufficient to allow us to recognize it as an early species of *Cosmomya*. It differs from *Cosmomya v-scripta* in having a less well marked posterior V in its ribbing. BM L46433 has more steeply dipping anterior transcurrent ribs than the other specimens and is in this way similar to the anterior flank of *Pentagrammysia*.

Genus ***SIPHOGRAMMYSIA*** Chernychev, 1950

TYPE SPECIES. *Pholadomya kasanensis* Geinitz 1880. Permian. ?Kazanian, Kazan, U.S.S.R.

DISCUSSION. *Siphogrammysia* resembles some other sanguinolitids in shape and has divergent ribs forming Vs in a similar way to *Cosmomya* and *Pentagrammysia* (Chernychev 1950; ?=*Manankovia* Astafieva-Urbaitis, 1983), but the discordant ribs are much bolder in design and more prominent. They are convergent in pattern with ribs of the trigoniacean, *Iotrigonia*, and a number of Unionacea including *Trigonioides*. A number of *Siphogrammysia* species have been described from the Upper Permian of Kazan and the Taimyr Peninsula. Here (Fig. 18) we illustrate some material from Malaysia which may be the same age.

Siphogrammysia* cf. *kasanensis (Geinitz, 1880) Fig. 18

cf. 1880 *Pholadomya kasanensis* Geinitz: 38–9; pl. 6, figs 23, 23a.
cf. 1894 ?*Goniomya kasanensis* (Geinitz); Nechaev: 314–16; pl. 10, figs 22, 26.
1950 *Siphogrammysia kasanensis* (Geinitz); Chernychev: 26–7; pl. 7, figs 61–3.

MATERIAL. BM PL5001 and BM PL5009, from Geological Survey of Malaysia locs. 106/RF/15 and 116/F/9; Labis area of Johore, Malaysia; in weathered silty shales associated with poorly preserved Ammonoidea, possibly mid-Permian *Agathiceras* sp.

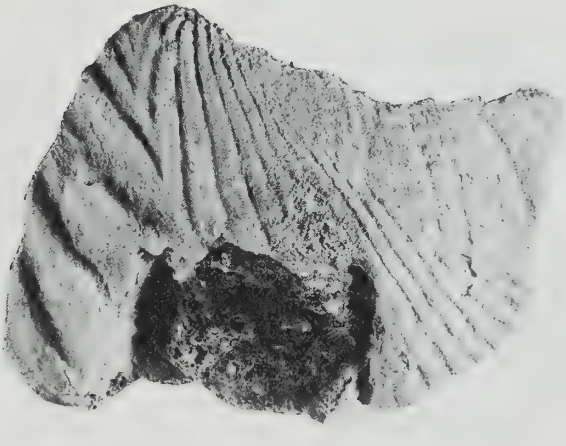


Fig. 18 *Siphogrammysia* cf. *kasanensis* (Geinitz). ?Upper Permian, Kazanian, Malaysia, locality 116/F/9B; BM PL5001; ×2·4.

DISCUSSION. The anterior flank of this species has prominent, broad transcurrent ribs which 'V' sharply, and near-vertical less prominent ribs below the umbones. A second V delimits the siphonal margin at its ventral point, with the V opening to the posterior. Yet a third V runs close to the dorsal part of the dorsal or siphonal area, again open to the posterior. This species differs from *Sanguinolites inordinata* Thomas (1928: 226–7; pl. 6, figs 8, 8b; pl. 8, fig. 7), which appears to be conspecific with *Goniomya kasanensis*, as interpreted by Lutkevich & Lobanova (1960:, 86; pl. 11, figs 1, 2), in having no break in the transcurrent ribs of the anterior flank. The latter two species clearly belong to *Cosmomya* rather than to *Siphogrammysia*, and are probably conspecific with *C. egraria* Holdhaus.

Genus ***GILBERTSONIA*** nov.

TYPE SPECIES. *Sanguinolaria gibbosa* J. de C. Sowerby, 1827, here designated.

DESCRIPTION. Nearly smooth, with comarginal growth lines and obscure comarginal ribs. No surface pustules observed. Umbones forward of mid-point, rounded and opisthogyral. A wide posterior dorsal area between the umbones and the siphonal margins joins the flank with a gentle change in shell slope, not defined by any feature of the ornament. Shell thin, inflated and elongate; striations on the inner shell surface possibly represent migrating points of mantle attachment. Anterior margin rounded and protruding; ventral margin sinuous, following a shallow, near vertical ventrolatera sulcus, sub-parallel to the hinge. Lunule distinct but not carinate, smooth; escutcheon long, narrow and carinate. The adductors are apparently sub-equal although the anterior one is not well preserved on any specimen we have examined. The posterior adductor is large, sub-rounded and spans the wide posterior dorsal area. The pallial line is without a sinus; it passes ventrally and posteriorly from the lower posterior edge of the posterior adductor parallel to the sloping posterior shell margins. The hinge plate is moderately thick, with a moderately long, very narrow, barely protruding nymph. The dorsal margins are opposed (adpressed) in a straight line well to the posterior. This indicates that they were joined by periostracal ligament.

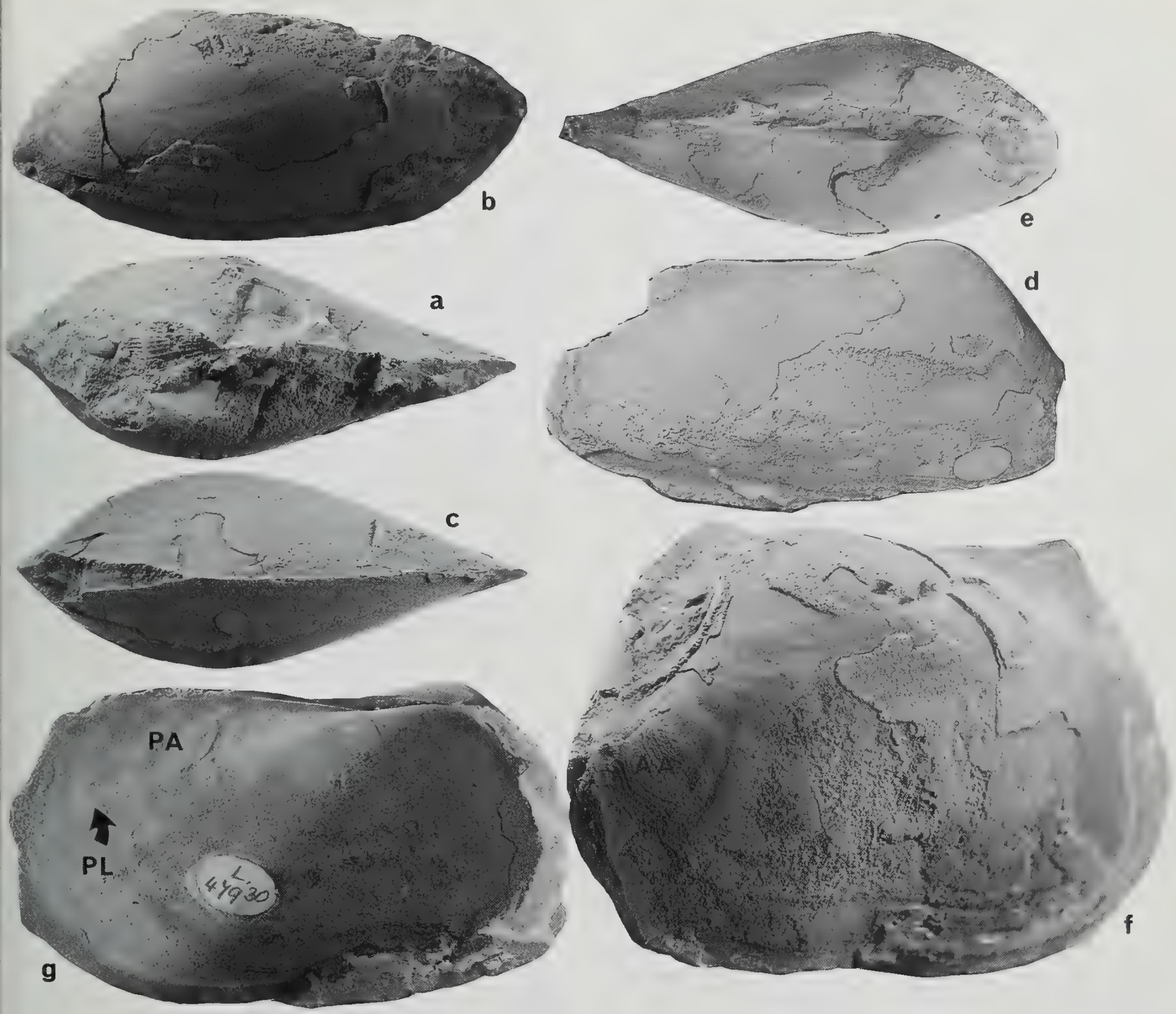
OTHER SPECIES. *Unio ansticei* J. de C. Sowerby (1840: pl. 39), and two apparently unnamed species from the Upper Carboniferous, Fort Jackson area, Texas.

REMARKS. *Gilbertsonia* resembles *Pachymya*, but that Mesozoic genus does not have a clearly defined lunule and has a much more robust ligament nymph and particularly prominent lines of shell surface pustules. Species of *Pachymya* are usually more thick-shelled than *Gilbertsonia*. The position of the posterior part of the pallial line also differs, and *Pachymya* has a shallow but distinct pallial sinus.

Eopleurophorus [Sanguinolites] hibernicus Hind has a very similar shell shape but a less sinuous ventral margin; it also has a posterior dorsal area with low ribs.

Gilbertsonia gibbosa (J. de C. Sowerby, 1827) Figs 19a–g

1827 *Sanguinolaria gibbosa* J. de C. Sowerby: **6**: 92; pl. 548, fig. 3.
1836 *Sanguinolaria tumida* Phillips: 209; pl. V, fig. 3.
1844 *Allorisma gibbosa* (J. de C. Sowerby); King: 315.
?1844 *Sanguinolites contortus* M'Coy: pl. 19, fig. 3.
?1885 *Sanguinolites luxurians* de Koninck: 73; pl. 16, figs 1–3.
?1885 *Sanguinolites tumidus* (Phillips); de Koninck: 81; pl. 16, fig. 6.



ig. 19 *Gilbertsonia gibbosa* (J. de C. Sowerby). Lower Carboniferous, Viséan. Figs 19a–c, 'Queen's County' (= County Laois), Ireland; BM 43056, holotype;) Fig. 19a, top; Fig. 19b, left side; Fig. 19c, bottom; all ×1·1. Figs 19d–e, Kildare, Ireland; BM L231, Tennant Collection; Fig. 19d, right side; Fig. 19e, top; both ×1. Fig. 19f, ?Bolland, Yorkshire; BM 97200, Gilbertson Collection, slightly oblique view of anterior of left valve showing anterior adductor; × 1·5. Fig. 19g, Kildare, Ireland, BM L47930, right side, with posterior adductor PA, and pallial line without pallial sinus PL.

1885 *Sanguinolites portlocki* de Koninck: 82; pl. 16, fig. 11.
1885 *Chaenomya requiana* (de Rychholdt); de Koninck: 7; pl. 1, fig. 11.
1900 *Sanguinolites luxurians* de Koninck; Hind: 402–4; pl. 46, figs 3–5.

IOLOTYPE. BM 43056 is the figured and only known ype specimen; from the Lower Carboniferous of 'Queen's ounty' (= County Laois), Ireland.

YPES OF *Sanguinolaria tumida* PHILLIPS. The specimen figured y Phillips (1836: pl. V, fig. 3) has not been discovered the Phillips collection at Oxford nor in the Gilbertson ollection at the BM(NH). Phillips said his figure was educed from a large Irish specimen. Specimens from the ilbertson collection listed as *S. tumida* in the Gilbertson Catalogue, but not labelled as such by Phillips and not belonging to the species as here understood (that is, not belonging to the same species as illustrated by Phillips), are not accepted here as syntypes. These include BM 97164 belonging to the species here recognized as *Myofossa omaliana* de Koninck (p. 63).

OTHER MATERIAL:

BM L231 from the Carboniferous Limestone of Kildare, Ireland; Tennant Collection, Fig. 19d–e (Hind identified this specimen as *S. luxurians*).

BM 97187 (41.6.7.132 in Gray Catalogue; 92g in Gilbertson Catalogue; *Isocardia* sp.; Phillips MS: pl. 5b, fig. 34; see below).

BM 36937, Carboniferous Limestone, Clane, Kildare, Ireland, Pratt Collection.

BM L13486, Carboniferous Limestone, Derbyshire, England.
BM L47930, Lower Carboniferous, Kildare, no other details.
BM L45242, Lower Carboniferous, St. Doolaghs, Co. Dublin, Ireland (labelled *Allorisma ansticei* Sowerby); Hind Collection.
BM(NH). Bancroft Collection no. 786, Clane, Kildare, Ireland.

REMARKS. Phillips' species *Sanguinolaria tumida* has to be interpreted from his figure (Phillips, 1836: pl. 5, fig. 3). Although we have been able to examine the mock-ups for the original plate (with kind help from Mr P. Powell of the Oxford University Museum) we have not been able to locate a type specimen, either in Phillips' own collection at the Oxford University Museum, or in the Gilbertson Collection at the BM(NH). The original manuscript and published figures seem to portray a species which may be considered to be a synonym of *Gilbertsonia gibbosa*. Unfortunately, the specimens in the Gilbertson Collection which we attribute to this species are not named as such in Gilbertson's manuscript catalogue, housed in the Palaeontology Library at the BM (NH). A further difficulty is that a specimen labelled no. 85 in the Gilbertson Catalogue, and there identified as *S. tumida*, is clearly not the specimen or species figured by Phillips; it is a *Myofossa omaliana* (p. 63). Hind apparently thought that the specimen BM 97200 was Phillips' figured specimen of *S. tumida*, but it does not have any individual features in common with the figure. We are therefore unable to identify any type material of *Sanguinolaria tumida* Phillips. Because we consider that species to be a junior subjective synonym of *Sanguinolaria gibbosa* J. de C. Sowerby, by identification of Phillips' figure with that species, we do not think it would be advantageous to create a neotype for Phillips' species. It is possible that *Sanguinolites luxurians* de Koninck, from the slightly older Calcschiste de Tournai, is the same species; but in de Koninck's figure the umbones are closer to the anterior. *S. luxurians* seems to have been based on only one specimen. De Koninck grouped his *S. luxurians* with species that have two diagonal folds (ribs?); if such ribs are present at all in *G. gibbosa* they are very indistinct. They are not at all comparable with the radiating sculpture that occurs on the corselet in some *Sanguinolites* and Permophoridae.

Sanguinolites contortus M'Coy may be a distorted specimen of the present species; we have not been able to examine the holotype. At present we treat *S. contortus* as a *nomen dubium*.

Subfamily **UNDULOMYINAE** Astafieva-Urbaitis, 1984

In this subfamily are placed *Wilkingia, Praeundulomya, Undulomya, Exechorhynchus, Dyasmya* gen. nov. and probably *Manankovia*. The subfamily contains elongate forms progressively adapted for deep burrowing. A lunule and escutcheon are present, with the ligament lodged in a groove at the front end of the escutcheonal area on a narrow ligament nymph. The external shell surface is granular, except for the escutcheon, with aligned periostracal spicules. Species of *Wilkingia* are known to have a deep pallial sinus. Runnegar (1969: 287, fig. 53c) records a pallial sinus in a specimen from the topmost Carboniferous or lowermost Permian of the U.S.A. The other characters of *Praeundulomya* and *Undulomya* link them to *Wilkingia*, from which we infer that they may also have had a deep pallial sinus. Just noticeable in *Wilkingia regularis*, but better developed in *W. maxima*, is a low, rounded, elongate rib present on the internal shell surface, running from the umbones towards the posterior margin. In *Praeundulomya* and *Undulomya* a second rib occurs, a little lower, which reaches the posterior margin at a point where the division between the two siphons would be expected. This feature also occurs in *Siliquimya*, ?Permophoridae.

The genera of this subfamily do not have the deeply inset anterior adductor, with a shell thickening immediately behind it, characteristic of *Siliquimya*. *Undulomya* has prominent V-shaped ribs, very similar to those in *Pentagrammysia* Chernychev, 1950, but that Carboniferous genus does not have the posterior interior radiating ribs that link it with *Praeundulomya* and *Wilkingia*. We therefore conclude that the V ribs have developed independently in this case. Astafieva-Urbaitis (1974*b*: fig. 1) illustrates a species from Kazakhstan with transcurrent ribs on the anterior only, intermediate between *Undulomya* and *Praeundulomya*. The Undulomyinae may be distinguished from *Vacunella* Waterhouse 1965 by the form of the escutcheon; in *Vacunella* the escutcheon does not have a sharp carinate edge and it is ill-defined distally where the dorsal margins pass evenly into the posterior siphonal gape. *Vacunella* also has much broader nymphs. *Myonia* Dana 1847, here also included in the Vacunellinae, has no pallial sinus.

Genus ***UNDULOMYA*** Fletcher, 1946

TYPE SPECIES. *U. pleiopleura* Fletcher, by original designation, = *Goniomya singaporensis* Newton, 1906.

Undulomya singaporensis Newton, 1906

?1906 *Goniomya scrivenori* Newton, 49: pl. 25, fig. 1.
1906 *Goniomya singaporensis* Newton: 493; pl. 25, figs 2–3.
1913 *Goniomya uhligi* Holdhaus: 450; pl. 94, fig. 2.
?1928 *Sanguinolites deportatus* Thomas: 229; pl. 6, figs 6.
?1928 *Sanguinolites insolitus* Thomas: 228–9; pl. 6, figs 11–12.
1946 *Undulomya pleiopleura* Fletcher: 399–400; pl. 34, figs 1–5; pl. 35, fig. 1.
1956 *Undulomya pleiopleura* Fletcher; Dickins: 29; pl. 4, figs 6–8.

TYPE MATERIAL. The two syntypes of *Goniomya singaporensis* are BM L19154, from the Permian, possibly Artinskian, Singapore (J. B. Scrivenor collection, *ex* Mr Guthrie) mistakenly described by Newton as Middle Jurassic; and BM L19173, part and counterpart of a fragment (Mr Hanitch collection). BM L19153 (apparently missing) is the holotype of *Goniomya scrivenori*. The holotype of *Goniomya uhligi*, from a geode in black shales below the Werfen Beds, NW of Kunplong, SW of the Niti Pass (horizon mistakenly doubted by Holdhaus (1913) and changed to Spiti Shales), is in the museum of the Geological Survey of India, Calcutta, and is from the same locality as *Cosmomya egraria* Holdhaus 1913. The type material of *Sanguinolites deportatus* and *S. insolitus* from the 'Goniatite Bed' and Steel Hill, Parinas Quebrada, Amatope Mountains, Peru, is in the Sedgwick Museum, Cambridge; it is probably Lower Permian in age, but it apparently associated in the collections with Pennsylvanian ammonoids.

REMARKS. This species has been well described and illustrated by Fletcher (1946), but examination of material from Singapore and Peru convinces us that it has a wide geographical range outside Australia and that there are a number of older names available for it. While the species has almost exactly the same shape a *Praeundulomya maxima*, with identical escutcheon and posterior internal ribs, it has developed a very pronounced V pattern of ribs with the line bisecting the angle of V sloping slightly backwards below the umbones. It is the similarities, coupled with what appears to be a good intermediate discovered by one of us (Astafieva-Urbaitis 1974*b*), which lead us to suggest the close relationship between the two genera. We have been unable to discover the posterior part of the pallial line in any of the material we have examined, but assume that the species would have been siphonate with a deep pallial sinus because that feature is present in the presumed ancestor and other members of the subfamily.

Genus ***WILKINGIA*** Wilson, 1959

TYPE SPECIES. *Venus elliptica* Phillips, 1836 (*non V. elliptica* Lamarck 1818), by original designation (as interpreted by Wilson, 1959; = *Allorisma regularis* King, *in* de Verneuil, 1845).

SYNONYMS. *Allorismiella* Astafieva-Urbaitis, 1962: 36 (type species by original designation, *Allorisma sulcata* Hind (1900: 42; pl. 48, figs 3–11), wrongly quoted as '*Allorisma sulcata* Hind, 1896'; this is not *Hiatella sulcata* Fleming, 1828 (see p. 57) and not *Allorisma sulcata* King, 1844: 316. We consider *Allorisma sulcata* as interpreted by Hind and Astafieva-Urbaitis to be a junior subjective synonym of *Allorisma regularis* King, *in* de Verneuil 1845 (see below), and a junior objective synonym of *Venus elliptica* Phillips, *non* Lamarck.

Dulunomya Astafieva-Urbatis & Dickins, 1984; type species by original designation *Dulunomya serpukhovensis* Astafieva-Urbatis & Dickins. We consider *Dulunomya serpokhovensis* to be a junior subjective synonym of *Allorisma regularis* King, *in* de Verneuil 1845.

REMARKS. In order to establish the identity of the nominal subgenera *Wilkingia* and *Allorisma* we have had to overcome a series of compounded errors and misinterpretations. King (1850: 196–9; pls 16, 20) clearly distinguished the characters of these taxa but unfortunately, by reference to misidentified type species, applied the names in reverse. From his footnote 1 on p. 196, however, it is clear that in his first publication (King 1844) he used the name *Allorisma* both for members of the family Edmondiidae and for forms with a deep pallial sinus here included in the Undulomyinae. Indeed the internal rib below the hinge is described as occurring in *Allorisma sulcata* (Fleming) (King 1844: 316). In 1850, King in effect changed his mind over the identification of *Allorisma* when he discovered that the characters of *Sanguinolaria sulcata* of both Fleming and Phillips resembled those of *Edmondia*, and differed from the siphonate forms here included in the Undulomyinae. His intention was to use *Allorisma* for the siphonate species (King 1850: pl. 20, fig. 5 only), but unfortunately he misidentified his material with the non-siphonate species *Allorisma sulcata* (Fleming, 1828) which he wrongly regarded as different from *Sanguinolaria sulcata* Phillips 1836 (see p. 58).

DIAGNOSIS. Lunule present and distinct escutcheon made up of an elongated flat area. Evenly rounded from front to back. Ribs constant in number. Pallial sinus deep.

DISCUSSION. In the Viséan and Namurian rocks, from the Moscow Basin to England and the U.S.A., there is a close knit group of species, which may only be distinguished in well-preserved specimens when subtle differences of shell shape and the form of the pallial sinus can be observed. These make up the genera *Wilkingia*, and *Praeundulomya* as here recognized. *Wilkingia* is of moderate size with sinuous ventral margins, and this group includes *W. regularis* and *W. ?transversa*. Species of *Praeundulomya* are large and include *P. maxima*, which has sub-parallel ventral and dorsal margins. The Permian *P. concentrica* also has this shape but is not so large.

It may prove in the future better to join *Wilkingia* with *Praeundulomya* as a junior subjective synonym, but at present we retain the two genera separated by the characters mentioned here.

Wilkingia regularis (King, *in* de Verneuil 1845)

Figs 20–24

?1836 *Venus elliptica* Phillips: pl. 2, fig. 7 (*non* Lamarck 1818).
1845 *Allorisma regularis* King, *in* de Verneuil: 298; pl. 19, fig. 6 only.
1850 *Allorisma sulcata* (Fleming); King: pl. 20, fig. 5.
1900 *Allorisma sulcata* (Fleming); Hind: 320, 422–4; pl. 48, figs 3, 5, 6, 9–11.
?1900 *Allorisma sulcata* (Fleming); Hind: pl. 48, fig. 8 only.
1900 *Allorisma variabilis* (M'Coy); Hind: pl. 48, figs, 1, 2 only.
?1950 *Tellinomorpha sarytschevae* Chernychev: 42; pl. 11, fig. 90.
?1950 ?*Tellinomorpha* sp. Chernychev: 43, fig. 92.
1959 *Wilkingia elliptica* (Phillips); Wilson: 402–4; pl. 71, figs 1, 3–6.
?1959 *Wilkingia elliptica* (Phillips); Wilson: pl. 71, fig. 2 only.
1962 *Allorismiella sulcata* (Hind) Astafieva-Urbaitis: 36.
?1962 *Allorismiella sulcata* (Hind); Astafieva-Urbaitis: 36–7, fig. 2.
1962 *Allorismiella regulariformis* Astafieva-Urbaitis: 39–40, fig. 2.
1984 *Dulunomya serpukhovensis* Astafieva-Urbaitis & Dickins: 38–9; pl. 2, figs 1–3.

TYPES. There are 12 syntypes in the de Verneuil Collection of the École des Mines (stored at present at the University of Lyon). Four of them are associated on a board bearing the register number 1743, and labelled '*Allorisma regularis* King, Sloboda, gouv. de Toula, Carbonifère. Coll. de Verneuil'; one of these is here selected lectotype (Fig. 20a–d), and the other three become paralectotypes. Other paralectotypes with similar locality labels are two specimens numbered 1744 and three specimens numbered 1745. Three more paralectotypes are on blocks numbered 1742 (two specimens; one of them was figured by de Verneuil (1845: pl. 21, fig. 11)) and 1746, labelled '*A. regularis* King, Valdai, Coll. de Verneuil'; we identify these three paralectotypes with the genus

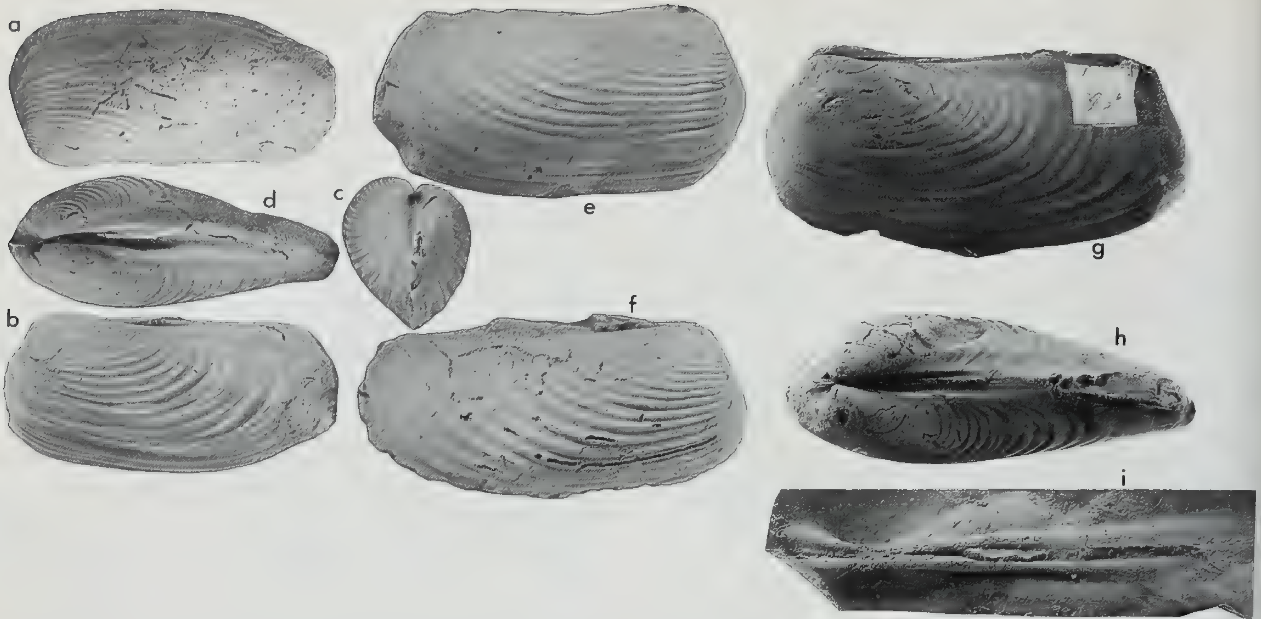


Fig. 20 *Wilkingia regularis* (King, *in* de Verneuil). Lower Carboniferous, Viséan; Sloboda, Gouv. de Toula, Russia. Figs 20a–d, EMP 1743 (1 of 4), de Verneuil Collection, **lectotype** (selected herein), a silicified steinkern; Fig. 20a, right side; Fig. 20b, left side; Fig. 20c, anterior; Fig. 20d, dorsum. Figs 20e–f, EMP 1744, paralectotypes, views of right sides. Figs 20g–i, BM L18, ? *ex* de Verneuil Collection, ?paralectotype; Fig. 20g, left side; Fig. 20h, dorsum; Fig. 20i, latex cast of hinge area seen from the inside to show inner surface of nymphs. All ×0·88, except Fig. 20i, ×1·5.

Allorisma King. Finally, two specimens (BM L18) in the BM (NH) that have the collectors' number 50, in similar handwriting to one of the Valdai specimens, may also be original syntypes that now become paralectotypes.

Synonyms. Although under normal circumstances we consider it inadvisable to designate types for junior synonyms or other invalid names, we feel that it is necessary to do this in the present case in order to preserve the stability of the generic name *Wilkingia*.

1. *Venus elliptica* Phillips, 1836 (*non* Lamarck, 1818). **Neotype**, here designated, is BM L47526, the specimen figured by Hind (1900: pl. 48, fig. 4). Wilson (1959: 402) designated the figure in Phillips (1836: pl. 2, fig. 7) as the lectotype of this species. In the same publication, however, he stated that the original specimen could not be found in the collections of the Yorkshire Philosophical Society (at the Yorkshire Museum, York) where it might be expected to be stored, nor in the Hancock Museum, Newcastle-upon-Tyne, nor in the University College Galway, Ireland. We have also been unsuccessful in finding the specimen in the Gilbertson Collection in the BM(NH) (it is not listed in Gilbertson's manuscript catalogue). We have also searched in vain in Leeds City Museum and in the Phillips Collection at Oxford University Museum. In a series of Phillips' original drawings and mock-up plates for the *Geology of the Yorkshire Coast* kindly made available to us by Mr P. Powell of the Oxford University Museum, an original drawing of *Venus elliptica* is preserved together with the information that this specimen came from Harelaw, Northumberland and was in the collection of the Rev. C. V. Harcourt. These Harcourt specimens should be in the York Museum, and we would like to thank Dr Pyrrah of that Museum for carrying out a further unsuccessful search.

   Unfortunately it is very difficult to determine the taxonomic position of Phillips' lost specimen from his figure. Its characters include the elliptical shape with a rounded, non-sinuous venter, small size, indication of a lunule and broad, regular, distinct comarginal rugae. If indeed it was an anomalodesmatid it could be a synonym of one of four taxa, *Sanguinolaria sulcata* Fleming, *Sanguinolaria maxima* Portlock, *Allorisma regularis* King or *Pholadomya omaliana* de Koninck. *Siliquimya plicata* (Portlock), even t this small size, has a distinctly more elongate shape and a sharper increase in curvature at the posterior ventral margin. In 1845, King (*in* de Verneuil) identified Phillips' species with one from Russia and indicated that it occurred in northern England. He used the name *Cardiomorpha sulcata* de Koninck 1842 for this species. In order to avoid further difficulty, the neotype chosen here makes *Venus elliptica* Phillips 1836 (*non* Lamarck, 1818) a subjective synonym of *Wilkingia regularis* (King, *in* de Verneuil 1845).
2. *Allorismiella sulcata* Astafieva-Urbaitis, 1962. In her original description of *Allorismiella*, Astafieva-Urbaitis designated *Allorisma sulcata* Hind as type species. Under ICZN Article 70c this must be construed as a deliberate misapplication of the name which Hind (1900) himself correctly attributed to Fleming 1828, but then misidentified. Following the provisions of this Article, the type species fixed by that action is deemed to be a new nominal species. In her original description, Astafieva-Urbaitis (1962: 40) referred to the specimens figured by Hind (1900: pl. 48 [pl. 18 cited in error], figs 3–11), the specimen figured by Fedotov (1932: pl. 10, fig. 5), and other specimens she had

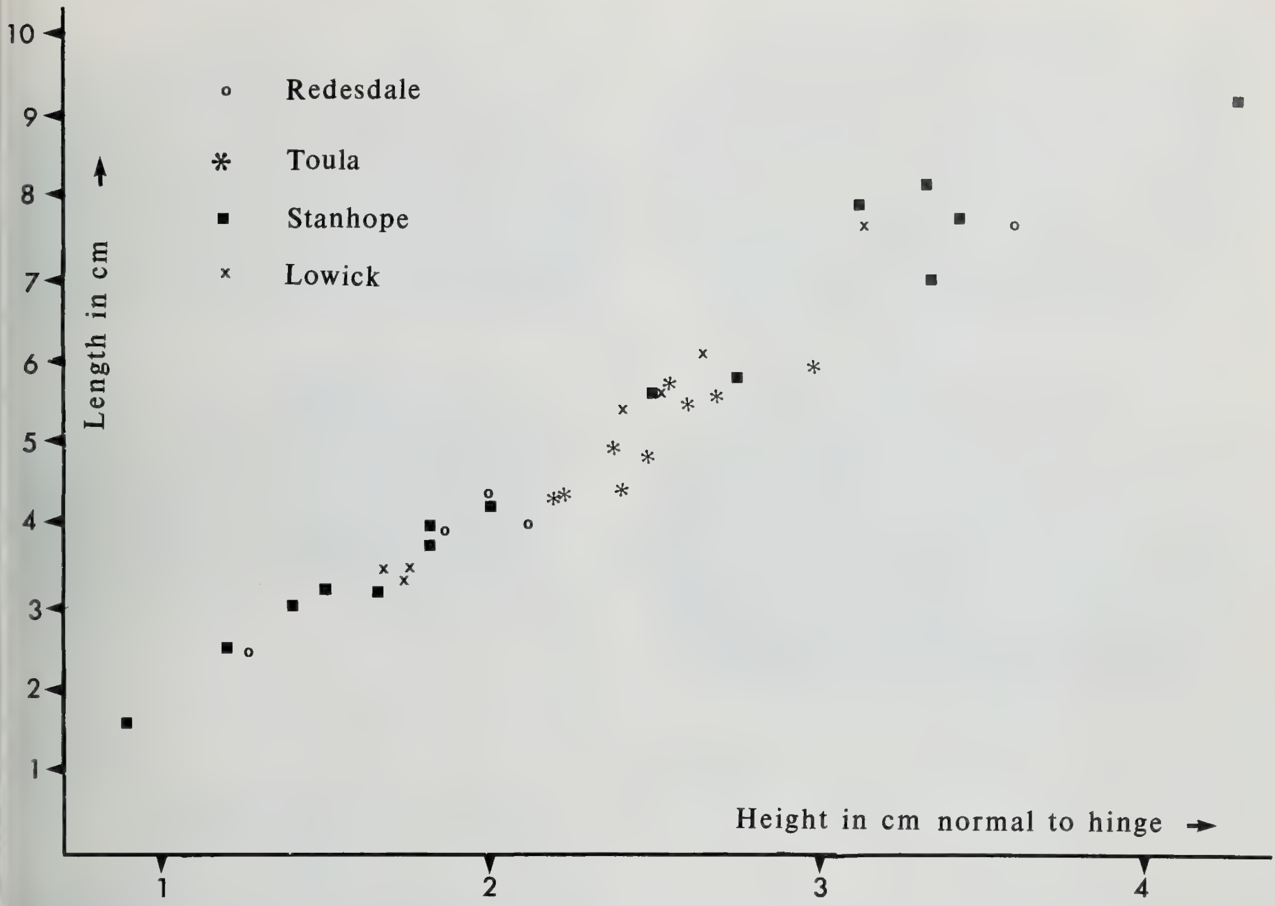


Fig. 21 *Wilkingia regularis* (King, *in* de Verneuil). Scatter diagram of height/length ratios of the four samples: (1) Redesdale Ironstone (Viséan) and (2) Main Limestone (Lower Namurian), both from Stanhope, Weardale; (3) Upper Viséan or Lowest Namurian, Lowick; (4) the type series from Sloboda (Viséan) (excluding specimens of *Allorisma*); this shows that the Redesdale material does not have a different height/length ratio from the other samples.

in front of her; all must be considered to be the type series of her new species. BM L47526, the specimen figured by Hind (1900: pl. 48, fig. 4), is here designated lectotype. By this action BM L47526 becomes the type specimen of both *Venus elliptica* Phillips (*non* Lamarck) and *Allorismiella sulcata* Astafieva-Urbaitis, so they are objective synonyms. Consequently the genera *Wilkingia* and *Allorismiella* become objective synonyms. In our opinion the valid name for the type species of *Wilkingia* Wilson is the oldest available subjective synonym, *Wilkingia regularis* (King, *in* de Verneuil, 1845).

MATERIAL. BM(NH): Hind Collection: Lower Limestone series, top Viséan (P2, D2 or D3, Brigantian); and Redesdale Limestone, L.-M. Viséan (B2 = D1, Asbian); Trechmann Collection: Main Limestone, Lowest Namurian, Stanhope, near Durham; and Viséan, Four Laws Limestone, Redesdale, Northumberland. EMP: de Verneuil Collection: mid-Viséan (said to be pre-Asbian), Sloboda, Toula, S. of Moscow. BGS: Redesdale Limestone, Northumberland (specimens figured by Wilson, 1959). SM: Lowick, Northumberland, Viséan.

DESCRIPTION. The shell is of medium size and very thin, resembling species of *Pleuromya* and early species of Panopeidae except that the dorsal margins extend in a straight line further towards the posterior. It is elongate with the umbones well towards the anterior. The ventral margin is sinuous, marking an obvious but gentle subumbonal sulcus. The maximum height is at about the mid-point, well to the posterior of the umbones. The umbones are slightly tumid and only slightly raised above the hinge line. The nymphs are relatively long and very slender, barely protruding from the long, straight, adpressed posterior dorsal margins, which themselves indicate that they were joined by periostracal ligament well towards the posterior margins. The hinge is edentulous. The musculature, including the pallial sinus, is illustrated in Fig. 22.

The comarginal rugae or ribs are a little irregular, but rather constant in number from front to back. They are in the form of shell corrugations, and apart from the barely discernible growth lines are equally well preserved on the steinkern and the shell surface. There are almost imperceptible radiating ridges on the steinkerns possibly reflecting lines of surface pustules that occur across the complete shell surface except within the escutcheon. The shell has a small lunule which has no carina, instead curving imperceptibly into the anterior part of the flank. The long narrow escutcheon is limited by a sharp carina, and there is a slight shell thickening, in the form of a

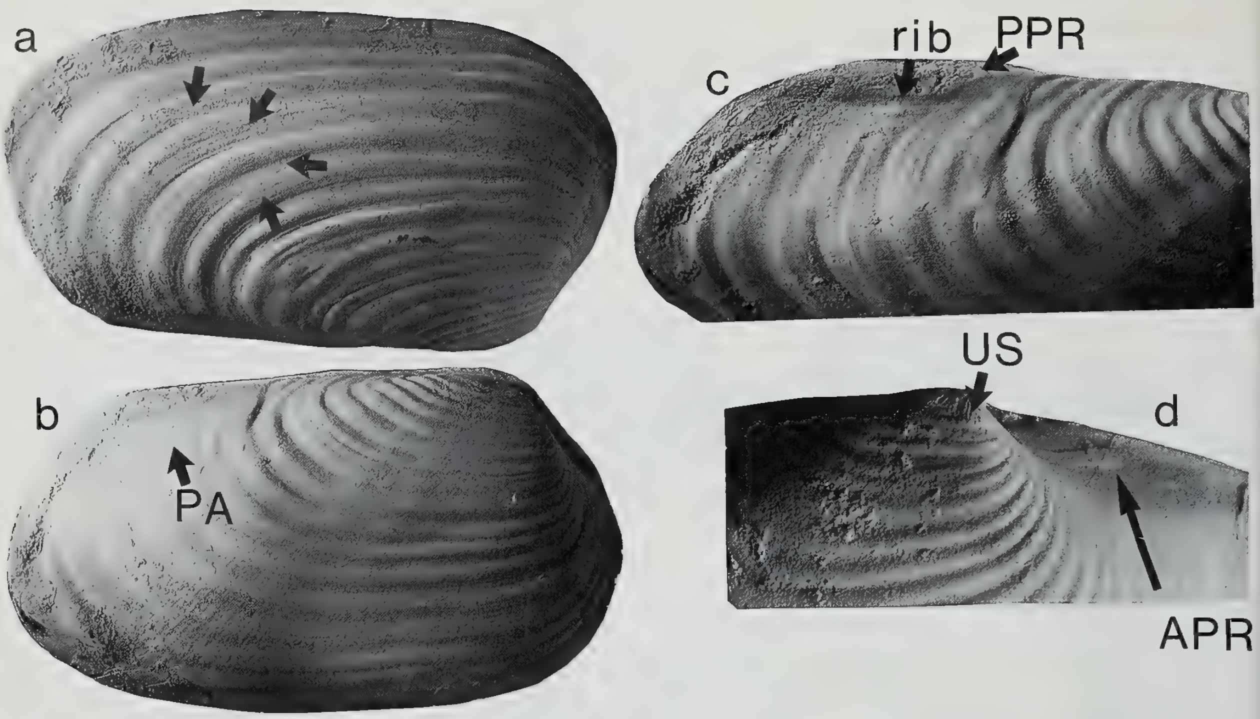


Fig. 22 *Wilkingia regularis* (King, *in* de Verneuil). Lower Carboniferous, Viséan (Asbian), Redesdale Ironstone, Redesdale, Northumberland. BM PL5002; Fig. 22a, left side, position of pallial sinus arrowed, periostracal pustules visible in postero-dorsal area, ×2; Fig. 22b, right side with posterior adductor (PA), ×2; Fig. 22c, oblique view of siphonal area of right side, showing posterior pedal retractor scar (PPR) and internal dorsal rib, approx. ×3; Fig. 22d, umbonal area viewed obliquely from top, showing scars of anterior pedal retractor (APR) and accessory umbonal scars (US), approx. ×4.

low internal rib, running at a very low angle from the umbo towards the posterior margin.

Remarks. Hind included *Posidonomya transversa* Portlock (1843: 174; pl. 38, fig. 9) in the synonymy of this species without comment. There is no indication from Portlock's figure that it belongs to this superfamily and we consider that Hind made a mistake. Another early nominal species that belongs in *Wilkingia, Lutraria primaeva* Portlock (1843: 441; pl. 34. fig. 5), was curiously interpreted by Hind (1900: 307) as an *Edmondia*. Hind went so far as to claim that another specimen had been substituted for the original, but it is clear that this is not so, from both Portlock's drawing and from his measurements. However, the measurements and the figure suggest that this species falls outside the variation of *W. regularis*, and it is probably a senior synonym of *Allorisma monensis* Hind. *Wilkingia regularis* differs from *W. primaeva* in being more elongate and having a differently shaped pallial sinus.

Hind (1900: 424; pl. 48, figs 1–2) described specimens of this species from Lowick and Calderwood as *Allorisma variabilis* (M'Coy). The lectotype of that nominal species (Fig. 17, p. 69) is, however, a crushed specimen of *Cosmomya*, also from Lowick. Amongst Hind's specimens, the ribbing on the umbonal area is only significantly irregular in the lectotype, and this is characteristic of *Cosmomya*. Most of the specimens of the present species, recognized by Hind as *Allorisma sulcata*, by Wilson as *Wilkingia elliptica* and by Astafieva-Urbaitis as *Allorismiella sulcata*, come from the Redesdale Ironstone, of high Viséan, Asbian, age, in

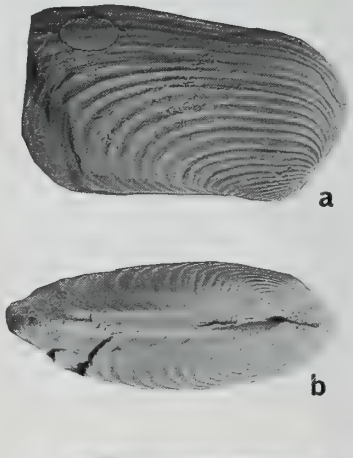


Fig. 23 *Wilkingia regularis* (King, *in* de Verneuil). Lower Carboniferous, Viséan (Asbian), Redesdale Ironstone, Redesdale, Northumberland. BM L45252, Hind Collection, **neotype** (selected herein) of *Venus elliptica* Phillips, 1836 (*non* Lamarck, 1818). Fig. 23a, left valve; Fig. 23b, dorsal view; Fig. 23c, right valve; all ×1.

Northumberland. The material available from this locality is often a little crushed, many of the specimens have eroded anterior and posterior margins, and many of the specimens are of small size. The limestone specimens from Lowick and Stanhope are better preserved and larger, as are the specimens from Sloboda in what used to be the 'Gouvernement de Toula', south of the Moscow Basin. The difference in preservation and size led Astafieva-Urbaitis to identify smaller gaping specimens as *A. sulcata*, distinct from *A. regularis* (1962: 36). We are uncertain whether or not these smaller Russian specimens belong to the same species. However, simple measurements of shell length and height (Fig. 21) suggest that the British specimens do not differ in these parameters, and they are also very close to the type material from the type locality of *Wilkingia regularis*. When Astafieva-Urbaitis introduced the name *Allorismiella* she was unaware that Wilson had at the same time been working on similar species and had introduced a new name three years earlier; she also had no opportunity to examine either Hind's material or the type series of *W. regularis*, which are the types of *Allorismiella* and *Dulunomya* respectively. She was working only with undescribed Russian specimens. Her holotype of *Dulunomya serpukhovensis* (Astafieva-Urbaitis & Dickins 1984: pl. 2, figs 1a–d) is identical in shape and sculpture to two of the paralectotypes of *Wilkingia regularis* (Figs 20e, 20f; those numbered 1744). Other specimens she refers to (Astafieva-Urbaitis, 1962: pl. 39, fig. 1) are apparently more closely related to the species described here as *Praeundulomya maxima* Portlock.

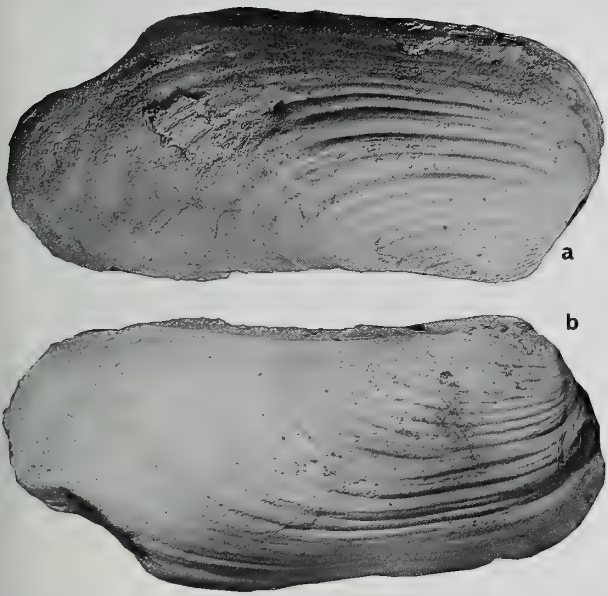


Fig. 24 *Wilkingia regularis* (King, *in* de Verneuil). Upper Carboniferous, Lower Namurian, Main Limestone, Stanhope, Weardale, Northumberland. BM PL5003; Fig. 24a, left side; Fig. 24b, right side; both ×0·9.

Genus *DYASMYA* nov.

TYPE SPECIES. *Allorisma elegans* King, 1850.

DESCRIPTION. Small to medium-sized undulomyine with sharp escutcheon and lunule. Escutcheon relatively wider than in *Wilkingia*. Subumbonal sulcus negligible or absent. Umbones more prominent than in other members of the subfamily. Anterior of shell prominent. The flatish posterior-dorsal or siphonal area is set off by a marked change in surface, forming a low rounded angle from the umbones to the posterior ventral margin, subcarinate. The shell structure of the type species is unknown but the outer surface bears very dense, close rows of small periostracal spicules. *Dyasmya* has a small but sharp pallial sinus, not much differing from that of a young *Wilkingia*. A small posterior gape is present. The comarginal rugae are less regular than those of *Wilkingia*, and in some specimens of the type species are barely present. The ligament is external, opisthodetic, parivincular, of medium length, mounted on narrow nymphs. The hinge plates are slender and parallel when viewed from above and without any teeth.

REMARKS. Beside the type species, the genus may include *Allorisma baldryi* Thomas, 1928, apparently from the Lower Permian of Peru; *Thracia longa* and possibly the more rounded *Thracia alta*, both of Lutkevich & Lobanova, 1960, from the Lower Permian of the Taimyr peninsular; and *Sanguinolites lunulatus* (Keyserling) as interpreted by those authors. Unfortunately the hinges of none of these species are known.

The more quadrate species of *Dyasmya* are very similar in outline to the Mesozoic genus *Pleuromya*, while the more rounded *Dyasmya alta* (particularly those individuals figured by Lutkevich & Lobanova (1960: pl. 11, figs 3–7)) resembles the Jurassic genus *Gresslya*. Both the Mesozoic genera have more advanced hinge types and a homogeneous inner ostracum, but they could have descended from *Dyasmya*.

The Jurassic species '*Pleuromya*' *angusta* Agassiz, 1843, commonly attributed to *Arcomya*, is very similar in shape but has many fewer rows of periostracal spicules. At present this seems to be the most suitable genus for Agassiz' species. We have observed a nacreoprismatic aragonite shell in specimens of this species in the BM(NH) from the Lias of southern England. *Arcomya* has an Upper Jurassic type species and is relatively longer and narrower, with a wide subumbonal sulcus sloping down and back below the umbones; it does not have the prominent umbones of *Dyasmya*.

Dyasmya elegans (King, 1850) Figs 25a–b

1850 *Allorisma elegans* King: 198; pl. 16, figs 3–5.
1967 *Wilkingia elegans* (King) Logan: 63–4; pl. 10, figs 6–10.

REMARKS. The shell has very dense, closely-packed lines of small, periostracal spicules, apparently over the total exterior surface of the shell. There is clear but fragmentary confirmation of the position of the pallial line as illustrated by Logan (1967: pl. 10, fig. 6a–b) in two of our rather poorly preserved internal moulds (BM PL96 and BM PL5006). These are from the lower part of the shell limestone of the Magnesian Limestone of Claxheugh Quarry, County Durham, England, and are apparently of Kazanian age.

We have no further information concerning this species beyond that available to Logan (1967) when he was preparing his monograph. We note, however, that it may well be intermediate between Carboniferous *Wilkingia* and the Mesozoic genus *Pleuromya*. *Pleuromya* has a form of pallial line and accessory muscle scars suggesting that it had a similar form of mantle fusion and siphon formation to the living

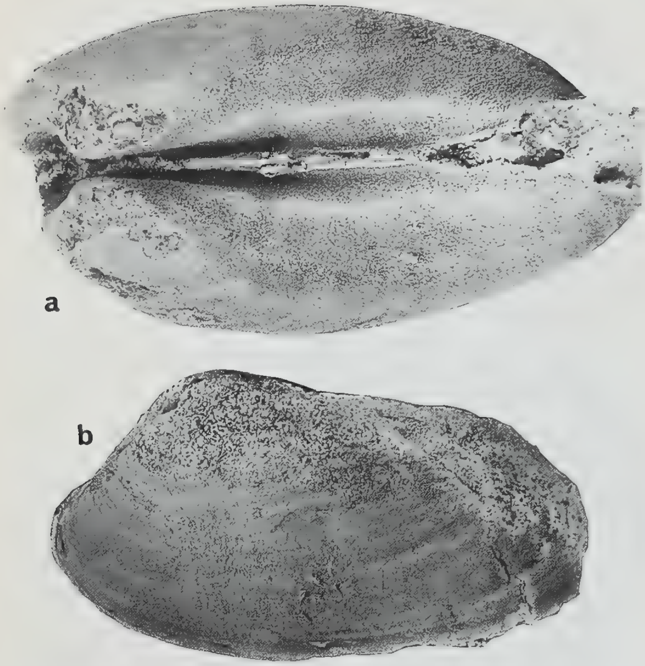


Fig. 25 *Dyasmya elegans* (King). Upper Permian, Magnesian Limestone, Claxheugh Quarry, Durham; C. T. Trechmann collection. Fig. 25a, BM PL5004, top view; Fig. 25b, BM PL5005, left side; both ×2.

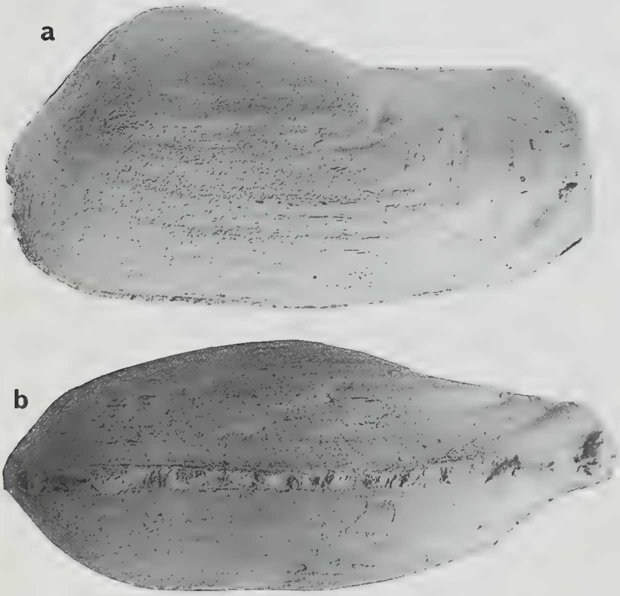


Fig. 26 *Wilkingia* sp. Lower Carboniferous, Kansas. USNM, no register number; Fig. 26a, left side; Fig. 26b, ventral view; both approx. ×0·8.

genera *Mya* and *Panopea*, differing somewhat in these features from the type species of *Wilkingia*. We have been unable to find additional material with these important details preserved. It may be important that the form of the escutcheon resembles that of *W. regularis* without the lateral separation of the dorsal shell margins typical of *Pleuromya* and other Myacea.

Genus *PRAEUNDULOMYA* Dickins, 1957

Type species. *Praeundulomya concentrica* Dickins 1957, by original designation.

Description. Transversely elongate, with well-developed escutcheon behind umbones in the form of a flat marginal area. The ligament proper was apparently lodged in a relatively short groove on the proximal edge of narrow nymphs close behind the umbones. The flat marginal area was probably covered and joined by periostracum, continuous with the ligament (see p. 54). The muscle scars are very shallowly impressed and a deep pallial sinus is visible in *P. maxima* and *P. subcuneata* (but not the type species). There are one or two ribs running below the hinge posterior to the umbones. These appear as grooves on the steinkern or composite mould, and are better developed than in *Wilkingia*. In the Permian species *P. concentrica*, the two posterior grooves are as well developed as they are in *Undulomya*. In outline from above, bivalved specimens have a distinctive tapering shape.

Praeundulomya is distinguished from *Wilkingia* essentially by the shape; in *Praeundulomya* the ventral and dorsal margins are sub-parallel with only a very slight subumbonal sulcus, whereas *Wilkingia* has a much more sinuous ventral margin. This difference is less obvious in young specimens.

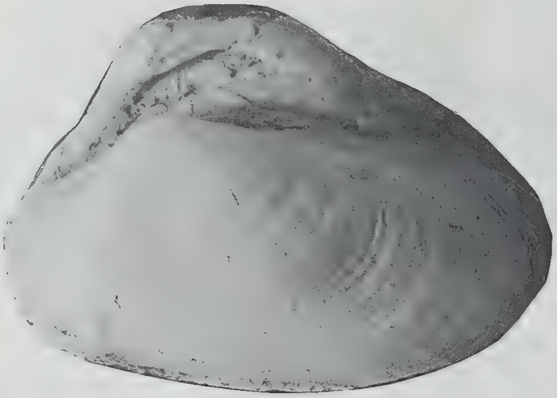


Fig. 27 *Wilkingia granosa* (Shumard). Upper Carboniferous, Pennsylvanian, 'Cisco, Graham', Young County, Texas. USNM Acc. 27130 (1 of 9), left side; the right valve is raised and shows the anterior part of the ligament nymph (the posterior part of the right valve is considerably eroded); ×1·3.

Remarks. Species here included as *Praeundulomya* have mostly been attributed to *Wilkingia* or *Dulunomya* by other recent authors. In the Gondwana area *Praeundulomya* seems to have been replaced by *Undulomya* and *Exochorhynchus* early in Permian time, before the begining of the Kazanian. The transition between *Praeundulomya* and *Undulomya* was demonstrated by Dickins (1957). Transitional species such as *U. insolitus* (Thomas, 1928) therefore indicate an age somewhere in the Upper Artinskian, following the correlation of Dickins (1963: 21). In the Amatope Mountains, Peru, Permian bivalves and Pennsylvanian ammonoids seem to be associated; this might be due to mixing during collection.

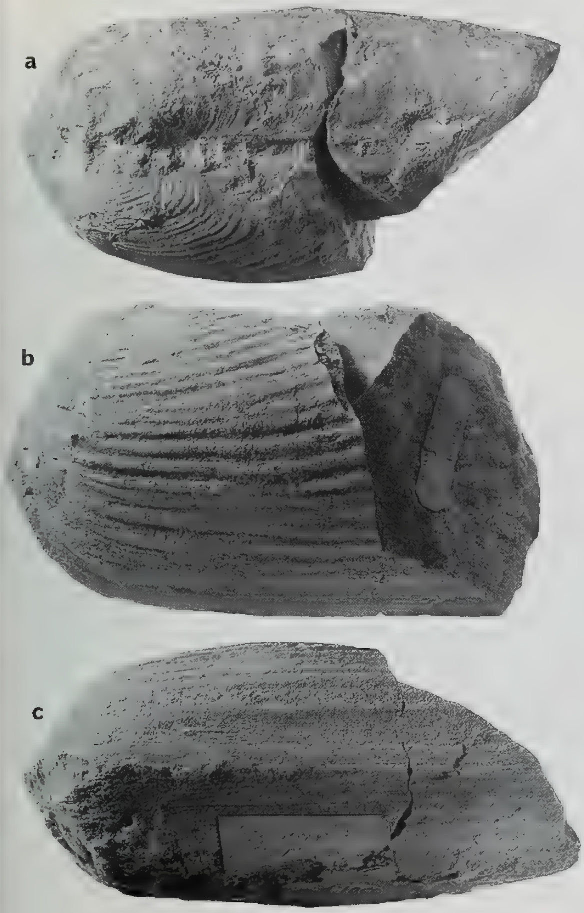


Fig. 28 *Praeundulomya maxima* (Portlock). Lower Carboniferous, Viséan, Donaghenry, Co. Tyrone, Ireland; BGS 6561, holotype; Fig. 28a, top view; Fig. 28b, left valve; Fig. 28c, ventral view; all ×0·88.

Praeundulomya maxima (Portlock, 1843) Figs 28–29

1843 *Sanguinolaria maxima* Portlock: 434; pl. 36, figs 1a, 1b.
1851*a* *Sanguinolites clava* M'Coy: 172.
1852 *Allorisma terminalis* Hall: 413; pl. 2, fig. 4a–b.
?1859 *Allorisma subcuneata* Meek & Hayden: 37; pl. 1, figs 10a–b.
1898 *Allorisma subcuneata* Meek & Hayden; Weller: 79–80.
1900 *Allorisma maxima* (Portlock); Hind: 419; pl. 47, fig. 5.
?1900 *Allorisma maxima* (Portlock); Hind: 419; pl. 47, figs 6, 7a, 7b.
1962 *Allorismiella regularis* (King); Astafieva-Urbaitis: 39, fig. 1.
?1974 *Wilkingia terminale* (Hall); Runnegar: pl. 1, fig. 31.
?1984 *Dulunomya maxima* (Portlock); Astafieva-Urbaitis & Dickins: 39.

HOLOTYPE. BGS (Leeds) 6561 (figured Portlock (1843: 434; pl. 36, figs 1a, 1b) and Hind (1900: pl. 47, fig. 5)), preserved in a light grey Carboniferous Limestone (possibly early Viséan), from Tyrone, Donaghenry, Co. Tyrone, Ireland.

OTHER MATERIAL. SM E1089, the type of *Sanguinolites clava* M'Coy 1851, and SM E1090, both from the Upper Grey Limestone, Upper Viséan, D2 (lower part of the Brigantian), at Llangollen, north Wales. SM E1090 is apparently slightly younger than the holotype.

DIAGNOSIS. Robust subquadrate species, with thin shell, ventral margin more or less parallel to the dorsal. Ornament of coarse, evenly rounded rugae parallel to the exterior, anterior and most of the ventral margins, but thicker and non-parallel at the posterior margin.

DESCRIPTION. Lunule and escutcheon present. Escutcheon made up of an elongate flattened area. Below the escutcheon there is a well-marked groove. The adductor muscles and the rear part of the pallial line are clearly visible in BM L47524. The anterior adductor muscle is rounded and slightly ovoid in a dorsoventral direction. Above is a small rounded scar, apparently of the anterior pedal retractor. The posterior adductor is high, rounded, but lightly marked. A deep pallial sinus is visible below the muscle scar. Thin shell is preserved in a few places. A small posterior gape was apparently present.

COMPARISONS. The specimens figured by Hind (1900: pl. 47, figs 6, 7) from the Viséan of Llangollen, north Wales, can be seen to have a slightly more sinuous posterior shell outline and have slightly less regular ribs than the holotype, even though the latter is not a complete specimen. At present we do not regard this as a specific difference. In fact specimens from the Upper Pennsylvanian of Texas named *Allorisma subcuneata* by Meek & Hayden (1858) more closely resemble the holotype. These younger specimens are usually a little smaller than *P. maxima*, but it is difficult to pick out any specific difference even in the best-preserved individuals. Also *Allorisma terminalis* Hall (1852) is probably a synonym of *P. subcuneata*. At present we do not have enough material on which to make measurements that might confirm our view that these species are similar in shape, and we tentatively include both as synonyms of *P. maxima*. Likewise we are unable to distinguish the two specimens from the Viséan of the Moscow Basin listed in the synonymy.

Praeundulomya maxima is very similar to the Permian type species *P. concentrica* Dickins 1957, but the latter has broader radiating internal posterior shell ribs. It also has comarginal low ribs that are more broadly spaced, which undergo low angular changes of direction in the lower part of the posterior or siphonal area. The pallial sinus of *P. concentrica* has not been observed although it is assumed to have been present, as an advanced character shared with *Wilkingia* and other species of *Praeundulomya*.

Genus ***EXOCHORHYNCHUS*** Meek & Hayden, 1865

TYPE SPECIES. ?*Allorisma altirostrata* Meek & Hayden, 1858, by original designation.

REMARKS. Examination of the type material of *E. altirostrata* in the United States National Museum led us to reject the use of this generic name, because all of the specimens were crushed and apparently foreshortened along their long axis, making it impossible to compare them with *Praeundulomya*.

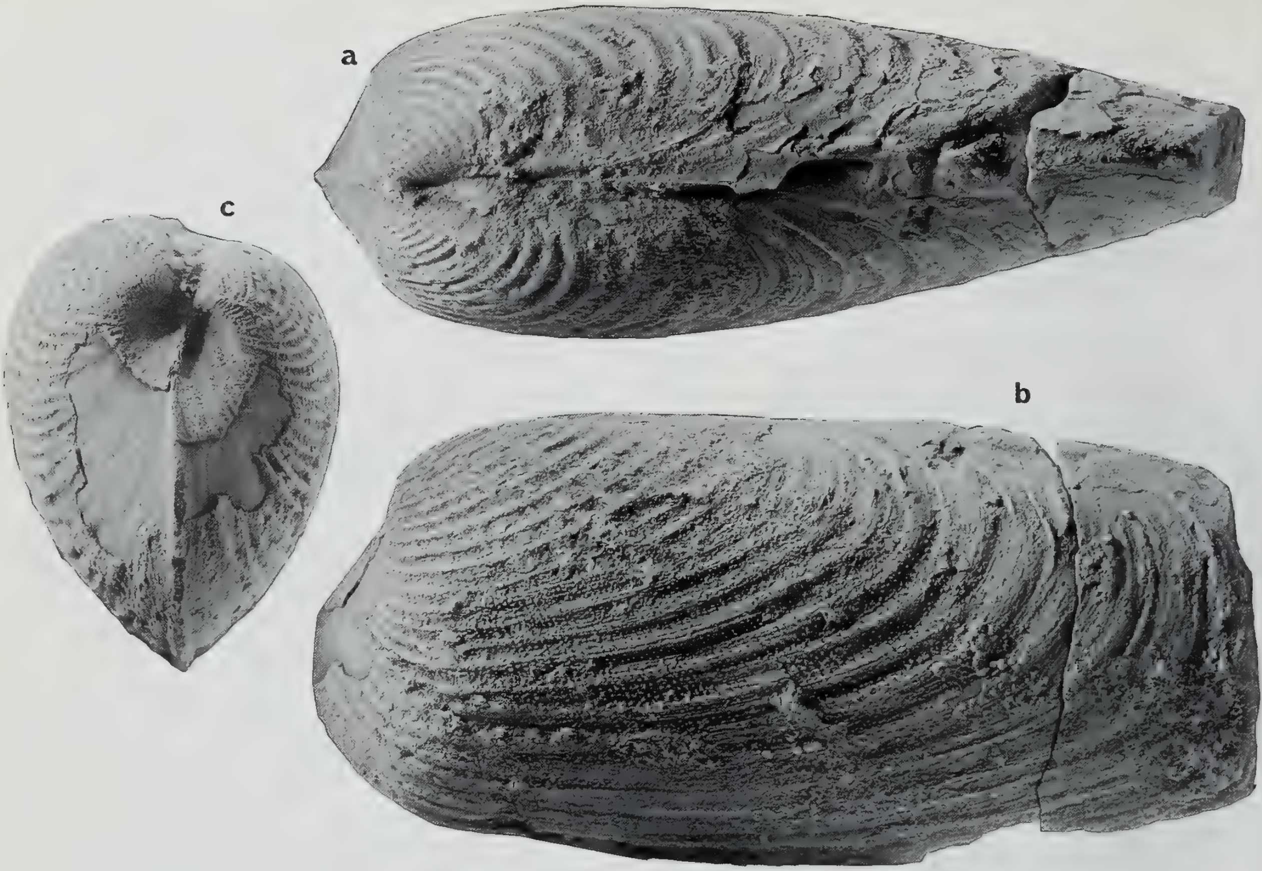


Fig. 29 *Praeundulomya maxima* (Portlock). Upper Carboniferous, Upper Pennsylvanian, Cisco Formation, near Jacksboro, Texas. BM PL5012. C. H. C. Brunton Collection (previously identified as *subcuneatus* Hall); Fig. 29a, dorsal view; Fig. 29b, side view; Fig. 29c, anterior view; all ×1·5.

Runnegar (1974) also took this view and rejected the name as a *nomen dubium*. However, our more recent examination of the type material of *Allorisma barringtoni* Thomas, 1928, first described as Carboniferous but here reinterpreted as Upper Artinskian, has shown us that there really are some species that have shells much shorter than *Undulomya maxima*, and which seem to be intermediate in form between Undulomyinae and the Mesozoic species of *Homomya* and *Pholadomya*. They also show no trace of the internal dorsal posterior ribs that are typical of *Undulomya* and *Praeundulomya*. For these reasons we resurrect the generic name *Exochorhynchus*.

Exochorhynchus barringtoni (Thomas, 1928)

Figs 30a–b

1928 *Allorisma barringtoni* Thomas: 221–2; pl. 7, figs 5, 6.
?1960 *Allorisma similis* Lutkevich & Lobanova: 83; pl. 10, figs 6–8.

Material. The holotype is SM A4948 (Fig. 30), and SM A4971 is one of several paratypes in the same collection; all are apparently from the Permian, probably the Upper Artinskian, of Sullana Rd., 1·5 miles south of El Muerto and Steel Hill, Parinas Quebrada, NW Peru, but (?wrongly) associated with mid-Pennsylvanian ammonoids when they were collected.

Description. A medium-sized species with rounded posterior and anterior margins and the ventral margin sub-parallel to the hinge line. The regular, low comarginal rugae are very similar to those of *Praeundulomya*. The posterior gape is very narrow and the narrow escutcheon is defined by a low, but distinct, carina. The umbones are well to the anterior, and the shell is apparently very thin.

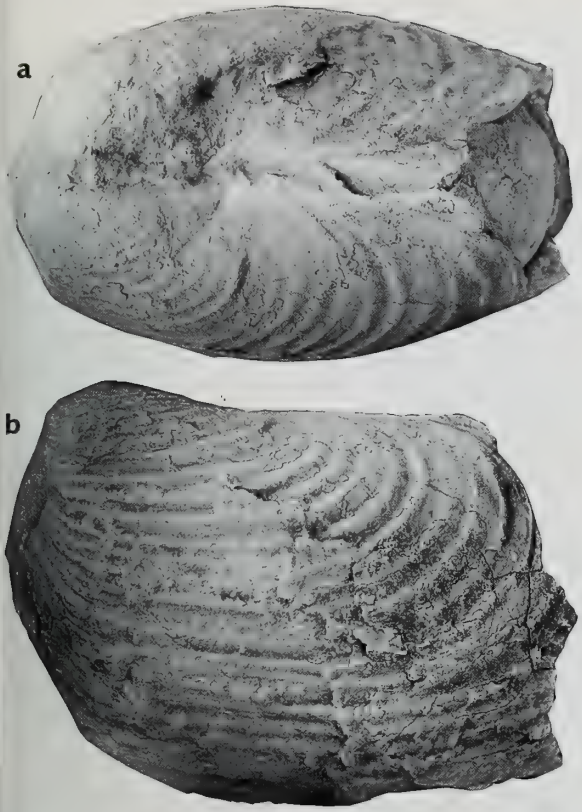
Remarks. *Exocorhynchus barringtoni* resembles the concentrically ribbed Pholadomyidae in the Triassic and it may be ancestral to them. There is also a considerable similarity to the Australian genus *Vacunella*. For the present, however, we follow the view of Runnegar and others that *Vacunella* developed independently in the Australasian area from some species of *Myonia* lacking a pallial sinus.

A number of similar species of *Exochorhynchus* have been described from Mongolia by Astafieva-Urbaitis (1981). The species described by Lutkevich & Lobanova (1960) from the Taimyr Peninsula of arctic Russia is somewhat distorted but has no features to distinguish it from the present species.

Subfamily **CHAENOMYINAE** Waterhouse, 1966

Genus ***CHAENOMYA*** Meek, 1865

Type species. ?*Allorisma leavenworthensis* Meek & Hayden, 1859, by monotypy.



ig. 30 *Exochorhynchus barringtoni* (Thomas). ?Lower Permian, ?Upper Artinskian, Sullana Road, 1·5 miles south of El Muerta Steel Hill, Parinas Quebrada, Amotape Mountains, NW Peru. SM A4971, paratype; Fig. 30a, dorsal view; Fig. 30b, left valve; both ×1·5.

ESCRIPTION. Medium-sized, elongate shells with the umbones bout half-way between the mid-point and the anterior nargins. Prominent rounded posterior gape present, of almost he full shell height. Hinge without teeth; a well-developed igament nymph extends for a short distance behind the mbones which supports a stout short C-spring ligament (see ig. 31). The rounded edges of the escutcheon fade half-way o the posterior margins, which diverge in a gentle curve to orm the top of the siphonal gape. The shell is thin and overed with regular rows of periostracal spicules.

OMPARISONS. *Chaenomya* Meek, 1865, has a broad posterior ape and hence, by comparison with living taxa, probably had ong, conjoined, periostacum-covered siphons. It does not, owever, have a deep pallial sinus, a feature we take to e a synapomorphy of the Undulomyinae, and we therefore onsider that it lies on a separate line of descent from *holadomya* and that subfamily. *Chaenomya* is very similar o the Jurassic genus *Osteomya* but we think that this is a case f convergence; *Osteomya* shares the transcurrent rugae on he anterior flank with the partly contemporaneous genus *lectomya*, which differs only in having a narrow posterior ape. *Chaenomya* has more prosogyral umbones than either *steomya* or *Plectomya*. There are comparable dense ustulose striae on the flank but these are much more rominent on the siphonal area of *Chaenomya* than either of he two Jurassic genera. The convergence probably reflects comparable increase in the development of the siphons. *Chaenomya* also shows convergence, in characters we associate with deep burrowing, with the Undulomyinae and the East Australian Permian genus *Vacunella*. Both of these taxa have a prominent inflexed pallial sinus and only a very modest posterior gape, which leads us to believe they belong to a different line of descent. It is possible that *Chaenomya* evolved from a species of similar shape and with a similar pallial line but without the wide posterior gape, such as the species described by de Koninck (1885) as *Chaenomya jacunda* (see p. 82 below). The wide posterior gape seems to be an alternative strategy of siphon formation to that of *Wilkingia* and *Pholadomya*, where in the living genus at least type 'C' siphons are developed with only a modest posterior gape. *Australomya* Runnegar (1969) is more compressed, lacks the distinct posterior or siphonal area and has a tendency towards opisthocline umbones. In this last character it resembles later genera such as *Thracia* and *Plectomya*. At present we are unable to ascribe more than this one species to the subfamily. Runnegar (1974: 928–9) also included *Cosmomya* in the Chaenomyinae, because he rejected the use of the name Sanguinolitidae, following his inclusion of *Sanguinolites* in the Grammysiidae.

Chaenomya leavenworthensis (Meek & Hayden, 1859)

Fig. 31

1859 ?*Allorisma leavenworthensis* Meek & Hayden: 263–4.
1865 *Chaenomya leavenworthensis* (Meek & Hayden); Meek: 42.
1967 *Chaenomya leavenworthensis* (Meek & Hayden); Runnegar: 63; pl. 11, figs 12–13.
1969*b* *Chaenomya leavenworthensis* (Meek & Hayden); Waterhouse: 38–9, figs 7J, 8I, 13; pl. 1, fig. 4; pl. 2, figs 5–9; pl. 3, figs 1–4, 7.
1974 *Chaenomya leavenworthensis* (Meek & Hayden); Runnegar: 929, text-fig. 5g; pl. 3, figs 5, 7.

MATERIAL. One specimen, USNM collection, from the Upper Carboniferous, at loc. 515g, Lower Graham Formation, 0·5 miles north of Texas 24, 6·5 miles west of Jacksboro, Texas.

REMARKS. This beautifully preserved specimen shows the distribution of spicules and the form of the ligament in perfect detail. The internal characters were well illustrated by Runnegar (1974: text-fig. 5g).

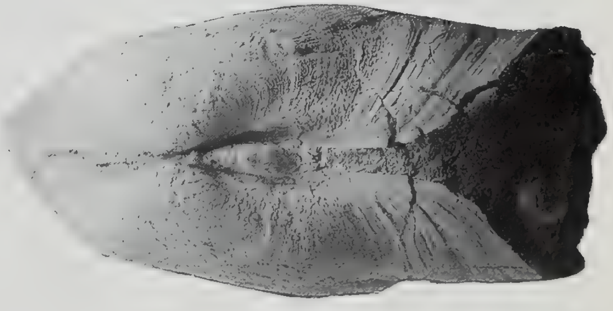


Fig. 31 *Chaenomya leavenworthensis* (Meek & Hayden). Upper Carboniferous, Lower Graham Formation, locality 515g, 0·5 miles north of Texas 24, 6·5 miles west of Jacksboro, Texas. USNM; with ligament and periostracal spicules preserved; dorsal view, approx. ×1.

Subfamily **ALULINAE** Maillieux, 1937

Remarks. These are elongate shells with an extended posterior. The shell surface bears rows of prominent periostracal pustules, which we interpret as a synapomorphy of the majority of the Anomalodesmata. The ligament is external, borne on a well-defined nymph and, most importantly, a well-formed cardinal tooth is present. The hinge of *Alula* is well illustrated by Runnegar & Newell (1971).

Genus ***TELLINOMORPHA*** de Koninck, 1885

Type species. *Tellinomorpha cuneiformis* de Koninck, 1885, by monotypy.

Comments. The elongate form and rudimentary cardinal tooth in the right valve link *Tellinomorpha* with the Alulinae.

Tellinomorpha cuneiformis de Koninck, 1885 Figs 32a–b

1885 *Tellinomorpha cuneiformis* de Koninck: 90–1, pl. 21, figs 1, 2.
1900 *Tellinomorpha cuneiformis* de Koninck; Hind: 433, pl. 49, figs 5–9.

Holotype. Musée nationale d'Histoire naturelle de Belgie, Brussels, no. 1698, from the Lower Carboniferous, Viséan, at Argenteau, near Visé, Belgium; this is the only known specimen.

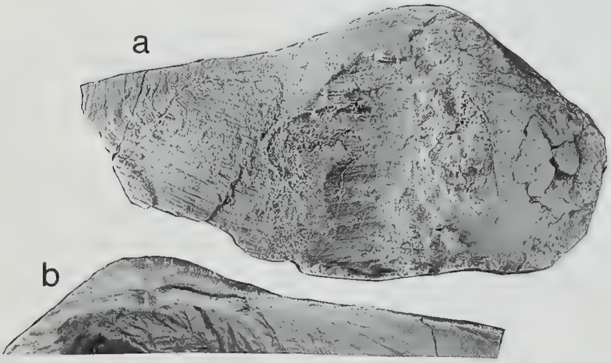


Fig. 32 *Tellinomorpha cuneiformis* de Koninck. Lower Carboniferous, Viséan, Argenteau, near Visé, Belgium. MNHN 1698, holotype; Fig. 32a, exterior of right valve; Fig. 32b, hinge area of interior of same valve, ×1.

Description. The holotype has the characteristic shape of a sanguinolitid, with a broad subumbonal sulcus and a sinuous ventral margin. The posterior part of the shell is attenuated, with the narrow siphonal area demarcated by the upturn of the growth lines. The siphonal margin has a slight median sulcus shaped so that two siphonal orifices are formed. The central surface of the flank has fine radiating striae which are, however, eroded and it is not certain whether or not they bore surface pustules. Irregular surface rugae are present indicating wrinkles in the periostracum. The hinge of the right valve (the only one known) has teeth below the umbo resembling those of some heterodonts and other groups where weak 'cardinal' teeth are present. The formula is RV (1) 0 1 0 N, which resembles some found in the trigoniacean family Schizodidae, but the arched gap or hiatus typical of the schizodids (Newell & Boyd, 1975: fig. 2) is not present, and *Tellinomorpha* has a very typical anomalodesmatid shape. The hinge is similar in the disposition of the teeth to that of *Alula* (figured by Runnegar & Newell, 1971: fig. 270) although they are less prominent, more like those of the Permophoridae. Simple teeth of this nature have apparently developed independently in a number of closely and distantly related stocks. *Tellinomorpha* does not have the elongate escutcheon typical of most Sanguinolitidae. The dorsal margin is apparently not parallel to the plane of commissure, indicating that there may have been both anterior and posterior shell gapes. There is a short, moderately stout ligament nymph behind the umbo, separated from the dorsal shell surface by a well-formed, narrow ligament groove.

Remarks. *Tellinomorpha* may be compared with '*Sanguinolites*' *clavatus* Etheridge 1877 (*non Allorisma clavata* McChesney 1860), but that species has an elongate, carina-bound escutcheon, indicating that the periostracal ligament joined the two valves back to the dorsal posterior margin, whereas the dorsal margins of *Tellinomorpha* apparently diverged posteriorly in a similar fashion to *Chaenomya* (Fig. 31). Examination of specimens from the Viséan Limestones of the Derbyshire Dome, England, attributed to *Tellinomorpha* by Hind (1900), show that these do not have the attenuated siphonal area of this genus and belong, in fact, to *Wilkingia*.

Subfamily Uncertain

An unnamed genus, intermediate in form between *Gilbertsonia* of the Sanguinolitinae and *Chaenomya*, is described here. It is possibly ancestral to *Chaenomya* or *Vacunella* or to both, and it includes the species '*Chaenomya*' *jacunda* de Koninck. Without further details of its characters we are uncertain in which subfamily it should be included.

Genus Uncertain

'*Chaenomya*' *jucunda* de Koninck resembles *Gilbertsonia* in shape but has a broad, shallow pallial sinus, somewhat resembling that of several species of *Myofossa* and *Cosmomya*. A narrow but obvious siphonal gape is present, which is about two-thirds of the total shell height, and therefore not as extensive as the posterior gape of *Chaenomya leavenworthensis*.

'*Chaenomya*' *jacunda* de Koninck, 1885 Figs 33a–d

1885 *Chaenomya jacunda* de Koninck: 7; pl. 1, figs 1–8.
1974 *Sedgwickia? jacunda* (de Koninck) Runnegar: pl. 3, figs 14–16.

Material. BM L13446, BM L13481, BM L47500 and BM PL1655, from the Lower Carboniferous, Viséan, at Tournai, Belgium.

Description. Medium-sized anomalodesmatid, gibbous with forward-pointing umbones well to the anterior. A small lunule is present with a subrounded carinate margin. The posterior dorsal margin is relatively long and straight, set in a broad escutcheon which is bounded by subrounded carinae. The siphonal margins are relatively long and straight, forming

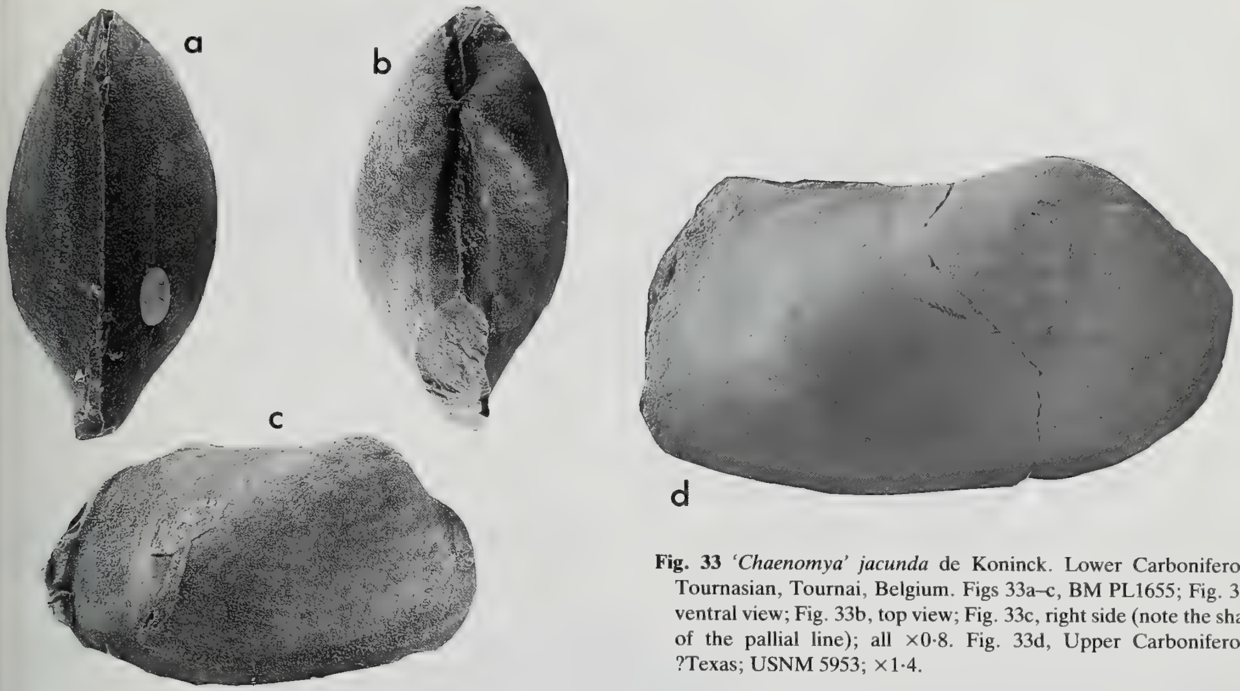


Fig. 33 *'Chaenomya' jacunda* de Koninck. Lower Carboniferous, Tournasian, Tournai, Belgium. Figs 33a–c, BM PL1655; Fig. 33a, ventral view; Fig. 33b, top view; Fig. 33c, right side (note the shape of the pallial line); all ×0·8. Fig. 33d, Upper Carboniferous, ?Texas; USNM 5953; ×1·4.

an obtuse angle with the hinge line. There is a moderate siphonal gape. The maximum width lies well to the posterior, but when viewed from above or below the shell at first narrows rapidly then straightens out towards the siphonal gape. There is a wide but shallow pallial sinus sub-parallel to the siphonal margin.

REMARKS. '*C.*' *jacunda* resembles some species of *Myonia* and *Vacunella* in shape and it is one possibility that it is their ancestor. An example (USNM 5952, Fig. 33c), possibly different, from the Upper Pennsylvanian of Texas, suggests hat this rather rare taxon may have had a considerable time range. '*C.*' *jacunda* is also closely similar to some species of he Mesozoic genus *Pachymya*, particularly *P. crassiuscula* Morris & Lycett, 1855) from the Bacocian of Normandy and England. '*C.*' *jacunda* is similar to *Myofossa omaliana* (de Koninck) in general shape and in the form of the pallial line. t is, however, much larger and does not have the opisthodetic umbones typical of *Myofossa*. The two could share close common ancestry.

Family **PERMOPHORIDAE** van de Poel, 1959

[*Pro* Pleurophoridae Dall, 1895; I.C.Z.N., Art. 40]

n the present paper we propose that the family Permophoridae hould be included with the Anomalodesmata rather than vith the heterodonts, as in the *Treatise* classification (Chavan, *n* Moore, 1969: N543). Aspects of the *Treatise* diagnosis of his family are, we suggest, an interpretation, based on its ssumed systematic position. The following phrases, quoted rom the *Treatise*, are clearly correct if the Permophoridae vere properly interpreted as carditaceans; in fact they are an xpression of the more obvious differences: 'Cardinals partly obsolete', 'radial ribs tending to be obsolete on anterior part of surface', 'anterior laterals lacking in most' (Chavan, *in* Moore, 1969; N543). The similarities between the Permophoridae and the Carditidae and the placing of the Permophoridae in the Carditacea depend upon the interpretation of the dentition. In heterodont terms, the teeth of the Permophoridae may be described as lucinoid when they are present. Bernard's analysis of heterodont teeth (1895), although of immense value in the Veneroida, is now suspected of supporting false homologies in the lucinoids (MacAlester 1966, Morris 1978). The considerable doubt concerning homologies of teeth between the heterodonts and the Trigoniacea had led Boyd & Newell (1968) to abandon the Bernard-Douvillé system for that superfamily and instead make use of a more objective (i.e. with no presupposition of homology) Steinmann notation. We suggest that the Permophoridae and the Carditidae belong to quite different subclasses of bivalves which separated before or at the very beginning of the Ordovician. If by some chance their cardinal teeth are homologous, which is unlikely on our present evidence, their form would be primitive for the two subclasses and would not indicate a close relationship between the two families. We think that the apparent similarity of tooth pattern in the two families is more likely to be the result of convergence. The number of possible teeth patterns is limited when there are fewer individual teeth. We therefore urge the use of the Steinmann notation for toothed forms of the Permophoridae. The true relationship of the Carditacea, we consider, has been recognized by Yonge (1969), who described the great similarity of 'mantle fingers' between the teeth in both Carditidae and Astartidae. The modioliform shape of some Maastrichtian to Recent Carditidae we would interpret as an advanced character because nearly all the earlier Cretaceous Carditidae are round in shape, resembling *Cyclocardia* and *Venericardia* and similar or more gibbous species of Astartidae, but with radiating ribs.

There is no clear evidence in the fossil record that the Cretaceous to Recent Carditidae are descended from those in the late Triassic. The fact that the Cretaceous carditids share most of their characters with the Astartidae leads us to believe that the Carditidae as presently recognized (Chavan 1969) are not a single clade. We believe that more than one group descended from ancestors at present classified with the Astartidae. They are, we believe, essentially 'Astartidae' which have developed radial ribs, a phenomenon that probably happened more than once. We therefore support Yonge's view that there is no need for two superfamilial names, Crassatellacea and Carditacea.

Most Permophoridae may be distinguished from most Mytiloida by the presence of a clearly-marked escutcheon and the fact that the external ligament is mounted on relatively short, upward facing, nymphs although there is considerable overlap between the two taxa in overall shell shape.

Subfamily **PERMOPHORINAE** van de Poel, 1959 (1895)

[*Nom. trans.* Chavan, *in* Moore 1969]

Genus ***PERMOPHORUS*** Chavan, 1954

Figs 34–35

TYPE SPECIES. *Arca costata* Brown, 1841, by monotypy.

REMARKS. The nomenclature of this genus is fully dealt with by Chavan in the *Treatise* (Chavan, *in* Moore 1969: N543). Examples of the type species and a similar species from the Permian of the Glass Mountains are figured here to show clearly the characteristics of the genus.

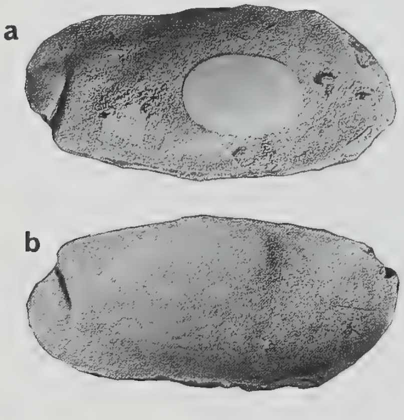


Fig. 34 *Permophorus costatus* (Brown). Upper Permian, Magnesian Limestone, England; BM PL235, steinkern; Fig. 34a, right side; Fig. 34b, left side; both ×1·5.

Licharew (1925: 125) proposed a new name, *Pleurophorina*, in which he included a single species, *Modiola simpla* Keyserling (1846: 28; pl. 10, fig. 22; pl. 14, fig. 1), which must, therefore, be the type of the genus by monotypy. The hinges figured by Licharew (1925: pl. 1, figs 1, 2) are close to *Permophorus* Chavan (1954) (pro *Pleurophorus* King, 1844, *non* Mulsant, 1842). If Licharew's specimens are correctly referred to *Modiola simpla* Keyserling, and we are not able to check on this, then *Permophorus* may be a synonym of *Pleurophorina*.

The shell is elongate-ovate with the umbones well towards the anterior. The rounded posterior margin and the area from it to the umbones is separated from the flank by a fine radial rib. There are sometimes further radial ribs on this posterior dorsal area. The flank and anterior are usually smooth. The hinge has an opisthodetic parivincular ligament set on slender short nymphs. Posterior lateral teeth occur, sometimes in each valve. The right valve has a single, moderately large cuneiform tooth which fits between the two subumbonal teeth of the left valve. These may be seen in the rather badly preserved steinkerns (Logan 1964) of *P. costata* but are better observed in *Permophorus* cf. *albequus* (Beede) (Fig. 35). The anterior adductor scar is of small to medium size, and deeply inset leaving a well-formed vertical buttress behind it. The posterior adductor is rounded and of medium size and set below the distal end of the posterior lateral tooth. The pallial line is entire although it is usually very faint towards the posterior of the shell.

Genus ***PLEUROPHORELLA*** Girty, 1904

TYPE SPECIES. *Pleurophorella papillosa* Girty, 1904, by original designation, from the Graham formation, Pennsylvanian (Cisco), of Young County, Texas.

SYNONYMS. *Eopleurophorus* Elias, 1957: 780 (type species, *Cypricardia? tricostata* Portlock (1843: 441; pl. 34. fig. 17) as interpreted by Hind (1900: 391), by original designation); from Carnteel, County Tyrone and Drumkeeran, County Fermanagh, Ireland.

DIAGNOSIS. Transversely elongate, distinct lunule and escutcheon, radiating ornament fairly well developed, especially in posterior part of shell. Granulation of shell surface by periostracal spicules distinct, apparently absent in some. More or less edentulous. Ligament lodged in a narrow elongated groove in the anterior part of a flat escutcheon which extends well towards the rear. Nymphs slender and low. The anterior adductor scar is well differentiated and bounded at the rear by a distinct buttress.

REMARKS. Chavan (1969: N546) placed *Pleurophorella* in the Permophoridae, though he expressed some doubt. We refer to this genus a number of Carboniferous species which have usually been referred to *Sanguinolites*; these include *Sanguinolites tricostatus* (Portlock, 1843), which is the type species of *Eopleurophorus* Elias (1957: 781), *S. striatolamellosus* (de Koninck, 1842), *S. striatus* Hind, 1900, *S. striatogranulatus* Hind, 1900, *S. visetensis* (de Ryckholt, 1847), *S. oblongus* Hind, 1900, *S. roxburgensis* Hind, 1900, and *S. ovalis* Hind, 1900. Other Carboniferous species are also included here.

Poor development or absence of teeth, together with the granulation of the shell surface, have perhaps hindered recognition of the relationships of this group. Genera of Permophoridae with well-developed lateral and cardinal hinge teeth share with the edentulous Carboniferous forms the distinctive lunule and escutcheon and the distinctly separated anterior adductor scar. The genus *Stutchburia* from the Lower to Upper Permian (see Dickins, 1963: 95) has poorly developed cardinal teeth and variable development of posterior lateral teeth, and occupies an intermediate position. The development of external granulation (pustules—a short rounded form of periostracal spicules) is apparently variable in both edentulous and tooth-bearing forms. Its presence or absence may also reflect preservation. In Permian and

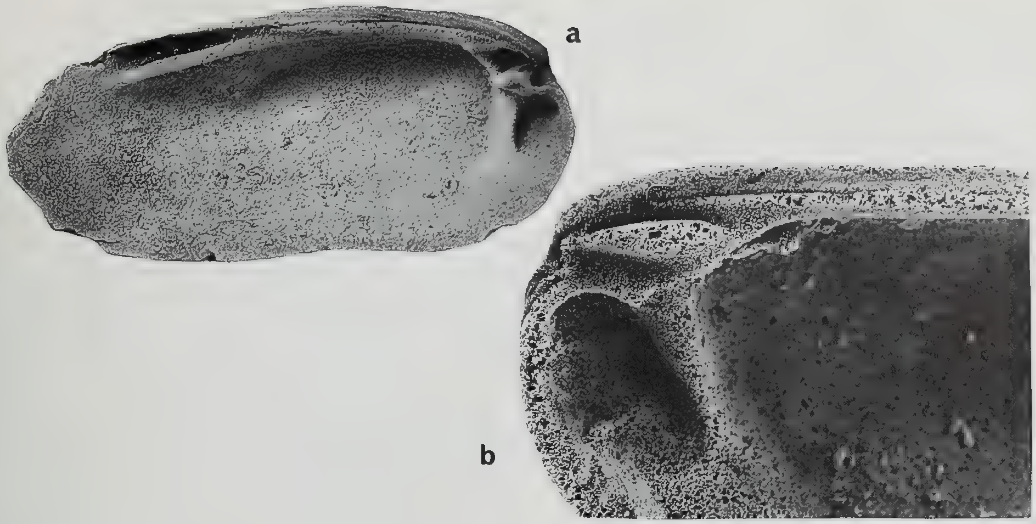


Fig. 35 *Permophorus* cf. *albequus* (Beede). Permian, West Texas; Fig. 35a, inside of left valve, ×4; Fig. 35b, umbonal area inside right valve, *c.* ×8. Photographs kindly provided by Professor N. Newell.

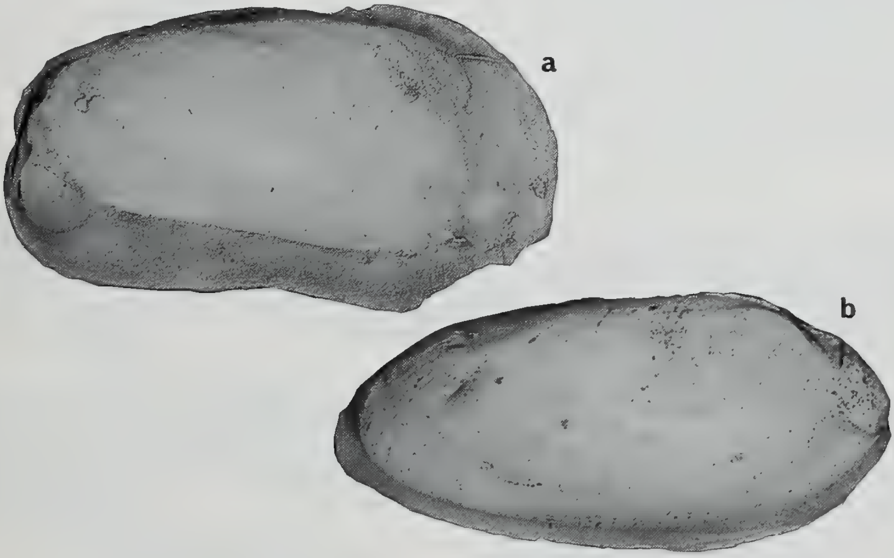


Fig. 36 Two species of *Stutchburia* with normal and unusual pallial muscle attachment. Fig. 36a, *Stutchburia farleyensis* (Etheridge); Lower Permian, Farley, New South Wales, Australia; BM PL603, with deeply inserted adductors and entire pallial line. Fig. 36b, '*Stutchburia*' sp.; Lower Permian, Bowen Coalfield, Queensland, Australia; BM PL539, with similar adductors and pallial line, but with an area of small spots, apparently of muscle attachment, below the posterior adductor, where a pallial sinus is found in many other bivalves; both ×1·5.

Triassic forms, granulation has been rarely recorded. Newell (1940: 298; pl. 3, fig. 16), however, described and figured irregularly occurring pustules in *Permophorus albequus* (see Fig. 35) from the Upper Permian of the USA, and Licharew (1925: 125) described granulation in *Pleurophorina* from the Kazanian of the USSR. From these data, it is reasonable to conclude that the forms with heterodont-like dentition are related to edentulous forms, and at present it appears that the edentulous Carboniferous forms are the more primitive in this respect.

Hind (1904) included two British Viséan species in the genus *Spathella* Hall 1885, '*Spathella*' *tumida* Hind and '*Spathella*' *cylindracea* (M'Coy). These seem to us to belong to *Pleurophorella*. Hinge details of *Spathella* are not well known, but Pojeta, Zhang & Yang (1986: 73) diagnosed the genus based on its type species as a lithophagiform modiomorphid with coarse comarginal ornament. This, and their illustrations of *Spathella typica* Hall, suggest to us that *Spathella* is not an anomalodesmatid and the two species were incorrectly placed in it by Hind.

Pojeta, Zhang & Yang (1986: 86; pl. 57, figs 5–8) also figured topotype material of *Sphenotus arcaeformis* Hall & Whitfield, 1869, the type species of that genus. They also followed Driscoll (1965) and others in ascribing to *Sphenotus* some species that we would attribute to *Pleurophorella*. When the hinge and musculature of *Sphenotus* *arcaeformis* are known it may well prove correct to synonymize *Pleurophorella* with *Sphenotus*; in the meantime we prefer to use *Pleurophorella*, where these characters are now known.

Pleurophorella papillosa Girty, 1904 Fig. 37

1904 *Pleurophorella papillosa* Girty: 729–32; pl. 45, figs 4–6; pl. 46, fig. 5.
?1969 *Pleurophorella papillosa* Girty; Chavan: N546.

MATERIAL. A single specimen, USNM G. A. C. Collection, from the Upper Pennsylvanian ('Upper Finis'), hills 0·5–1 mile north of a point 0·3 miles north-east of intersection of old Chico road and Wizard Wells Road, 3·2 miles east of Jacksboro, Texas.

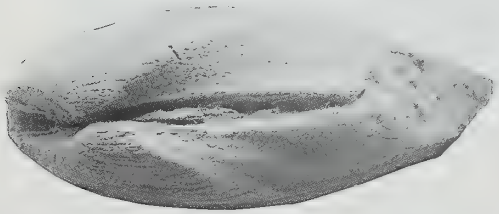


Fig. 37 *Pleurophorella papillosa* (Girty). Upper Carboniferous, Upper Pennsylvanian, Upper Finis Shale; hills 0·5–1 mile north of a point 0·3 miles NE of intersection of old Chico Road, 3·2 miles east of Jacksboro, Texas; USNM, G.A.C. Collection; dorsal view with ligament in place; *c*. ×1.

DIAGNOSIS. Shell surface with fine, close-packed pustules all over, otherwise without ornament. Nymphs slender and long, nearly half the length of the escutcheon.

REMARKS. We figure a specimen (Fig. 37) that conforms to Girty's original description and comes from the same area and horizon. It shows the nature of the nymph, occupying the anterior part of the escutcheon, and the surface is covered with fine close-packed pustules which seem to us to be merely low rounded periostracal spicules that do not show any particular alignment.

Pleurophorella tricostata (Portlock, 1843) Figs 38a–i

1843 *Cypricardia? tricostata* Portlock: 441; pl. 34, fig. 17.
1900 *Sanguinolites tricostatus* Portlock; Hind: 391–3.
?1900 *Sanguinolites striatogranulatus* Hind: 393–4; pl. 42, figs 16–22.

HOLOTYPE. BGS 14747 (Figs 38a, b).

OTHER MATERIAL. BM L13446, Carboniferous Limestone, Britain (no further details recorded); BM 22545 and BM L13481, J. Wright Collection, Carboniferous Limestone, Little Island, County Cork; BM L47500, Hind Collection, Poolvash, Isle of Man; all are from the Viséan. BM L24821–3 (Gilbertson Collection no. 97) are three syntypes of *Cypricardia glabrata* Phillips, 1836, that could be young

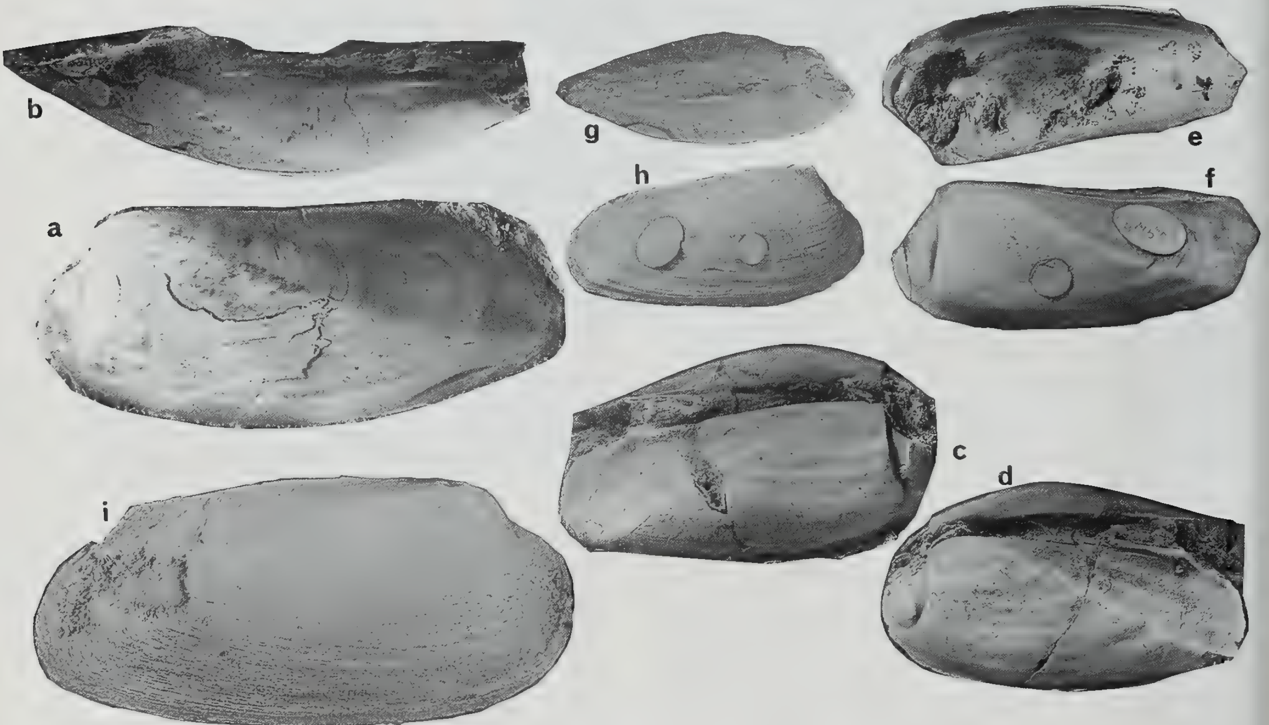


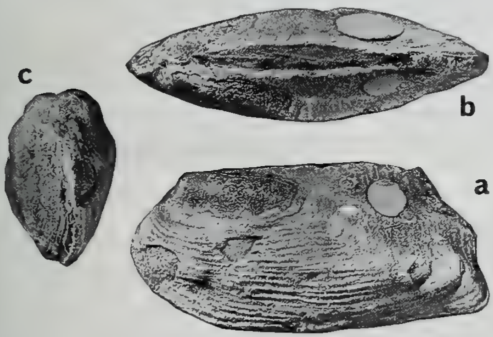
Fig. 38 *Pleurophorella tricostata* (Portlock). Lower Carboniferous, Viséan. Figs 38a–b, County Fermanagh, Northern Ireland; BGS 14717, holotype; Fig. 38a, left valve, side view; Fig. 38b, left valve, dorsal view; both ×1·6. Figs 38c–h, three syntypes of *Sanguinolites striatogranulatus* Hind; Figs 38c–f, Poolvash, Isle of Man; Figs 38c–d, BM L47500; Fig. 38c, right side; Fig. 38d, left side; both ×1; Figs 38e–f, BM L47502; Fig. 38e, right side; Fig. 38f, left side; both ×1; Figs 38g–f, Stebden Hill, Yorkshire, England; BM L47499, with shell preserved; Fig. 38g, dorsal view; Fig. 38h, right valve; both ×0.9. Fig. 38i, Little Island, County Cork, Ireland; BM L24545, ×1·8.

ndividuals of this or a number of other British species. As we are unable to decide to which of the smoother species they belong, we provisionally reject Phillips' species *Cypricardia glabrata* as a *nomen dubium*.

DESCRIPTION. Both the lunule and the escutcheon are defined by a distinct carina. The escutcheon is two-thirds of the shell length and the distance from the umbones to the posterior margins is five-sixths of the shell length. The dimensions of specimen BM L24545 are: L 42 mm, H 28·5 mm, U-P 35 mm. The umbones are prosogyral and confluent with a convex dorsum on both valves, whereas *Sanguinolites* is concave in this area. The ligament nymph is visible in BM L13446 and BM L13481; it is separated from the dorsal edge of the escutcheon by a distinct narrow groove, and its dorsal margin lies just below the margin of the escutcheon.

The internal surface is visible in BM L47500. The anterior adductor is well impressed into a raised area of the inner shell surface. The pallial line is partly visible in this specimen but is very faint; it does not have a sinus. Two radiating, fine, low ribs are present between the escutcheon and the low radiating line delimiting the corselet, which distinguishes the species from *Pleurophorella visetensis* de Rychkholt (*sensu* Hind, 900) which has three such ribs.

Closely related species which are not thought to be ynonyms are: *Sanguinolites striatolamellosus* de Koninck, *ensu* Hind (1900: 398; pl. 43, fig. 11 & 11a) (Fig. 39) (*non Cypricardinia striatolamellosa* de Koninck, 1842: pl. H, fig. 3a–c); *Isocardia transversa* de Koninck (1842: pl. 1, fig. 3a–b); *Sanguinolites oblongus* Hind (1900: pl. 43, figs 6–7); and possibly *Sanguinolites visetensis* (de Rychholt, 1847) *sensu* Hind (1900: 395; pl. 43, figs 1–4). We consider, however, that *Sanguinolites striatogranulatus* Hind (1900: 393; pl. 42, figs 6–22) may well be a synonym and the differences in shape and granulation may reflect preservation rather than specific differences.



ig. 39 *Pleurophorella striatolamellosa* (de Koninck). Lower Carboniferous, Viséan, Stebden Hill, Yorkshire; BM L47510; Fig. 39a, left valve; Fig. 39b, dorsal view; Fig. 39c, anterior view; all ×1·25.

***Pleurophorella* sp.** Fig. 40

MATERIAL. USNM 515g, two specimens from the Lower Graham Formation, Upper Pennsylvanian, 0·5 miles north of Texas 24, 6·5 miles west of Jacksboro, Texas.

DESCRIPTION. Shell ornament consisting of concave-upwards, harp, comarginal ribs with intervening fine growth laminae. No surface pustules are preserved. Carinate lunule and scutcheon present. The carina bounding the escutcheon is crenulate with prominent backward-pointing growth lines. The hinge of the right valve is particularly well preserved (Fig. 40); there is a small anterior tooth, parallel to the anterior dorsal margin, and a thin posterior tooth running parallel to and below the ligament nymph. The nymph is moderately long. It is not well preserved at its proximal end, where there may have been an attachment of the outer anterior ligament. The ligament groove is well preserved, and the ligament is present at the distal end; more proximally the upper surface of the nymph is transversely striate where part of the inner ligament layer has broken away. Growth laminae are visible on the inner surface of the nymph just below the attachment area of the inner ligament.

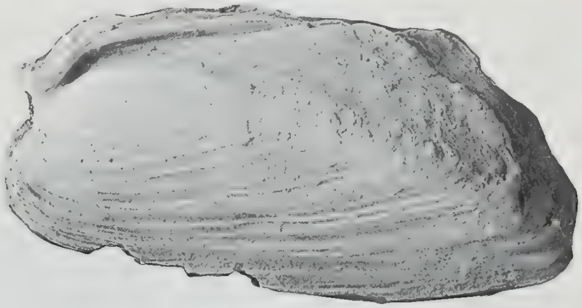


Fig. 40 *Pleurophorella* sp. Upper Carboniferous, Upper Pennsylvanian, Lower Graham formation, 0·5 miles north of Texas 24, 6·5 miles west of Jacksboro, Texas; USNM 515g, external view of left valve together with hinge of right valve; ×1·25.

REMARKS. *Pleuphorella* sp. is closely similar in morphology to *Stutchburia*.

Pleurophorella transversa (de Koninck, 1842) Fig. 41

1842 *Cypricardia transversa* de Koninck: 94; pl. 1, fig. 3; pl. 3, fig. 8.
1842 *Isocardia transversa* de Koninck: pl. 1, fig. 3 only.
1885 *Sanguinolites transversus* (de Koninck); de Koninck: 76; pl. 17, figs 4–5.

MATERIAL. BM 32908, de Koninck Collection, is a single specimen associated with an original label in de Koninck's

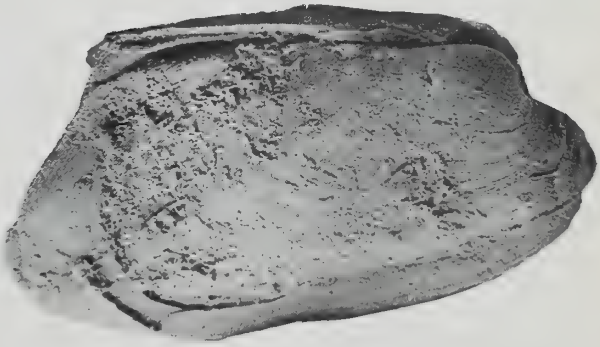


Fig. 41 *Pleurophorella transversa* (de Koninck). Lower Carboniferous, Tournaisian, Tournai, Belgium; BM 32908, de Koninck Collection, ?syntype, slightly oblique view of right side to show posterior lateral tooth of left valve in its correct orientation; ×2·5.

hand reading '*Cypricardia transversa* de Kon.' It is similar in shape and proportions to de Koninck's original figue, but with the valves slightly displaced, and it might be the figured syntype. A second specimen, a steinkern, bearing the same number appears to have been misidentified.

REMARKS. The displacement of the two valves has now exposed part of the hinge of the left valve (Fig. 41), which has a long, narrow hinge plate set into a long narrow carinate escutcheon. There is a slender short 'posterior lateral tooth' that we believe to have developed independently from similar teeth in the heterodonts. There is also a short nymph exposed which runs for a short distance behind the umbones, separated from the shell surface of the escutcheon by a marked ligament groove.

?Pleurophorella cuneata (Phillips, 1836) Fig. 42

1836 *Nucula cuneata* Phillips: 210; pl. 5, fig. 14.
1897 *'Nucula' cuneata* Phillips; Hind: 205.

HOLOTYPE. BM 97147, Viséan, Bolland, Yorkshire; Gilbertson Collection.

REMARKS. This tiny specimen has umbones at the anterior where it is cordate in section. The dorsal and ventral margins diverge slightly so the greatest height is towards the posterior. The posterior margins are rounded. The shell is very similar in form to a date mussel, except that there is a clearly marked elongate carinate escutcheon, typical of the Permophoridae. The similarity of form to a date mussel raises the possibility that ?*Pleurophorella cuneata* was also a rock borer.

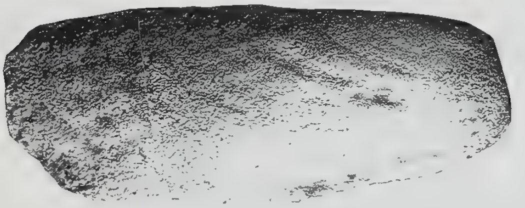


Fig. 42 ?*Pleurophorella cuneata* (Phillips). Lower Carboniferous, Viséan, Bolland, Yorkshire; BM 97147, Gilbertson Collection, holotype; approx. ×8.

Genus ***BOWLANDIA*** nov.

TYPE SPECIES. *Cypricardia rhombea* Phillips, 1836.

ETYMOLOGY. The generic name is derived from the Forest of Bowland, Yorkshire, an area locally famous for its Carboniferous fossils.

SYNONYM. *Ivanovia* Astafieva-Urbaitis, 1978 (*non* Dubrolyubova, 1935), type species, *I. slovenica* Astafieva-Urbaitis, 1978, by monotypy. See below.

NOMEN DUBIUM. *Digonomya* Whidborne 1897: 16–17 (type species, *D. elegans*) is superficially similar to the present genus. The type material is in the BGS collections but shows none of the characters of the hinge and is not well preserved; on this account we reject the generic name *Digonomya* as a *nomen dubium*.

DIAGNOSIS. The new genus resembles *Pleurophorella* but it has a relatively reduced anterior ventral margin giving it an overall modioliform appearance; we interpret from this that *Bowlandia* had a semi-infaunal byssate to epifaunal byssate habit, much like living *Mytilus edulis*, except that we have no evidence that the genus occurred intertidally. The anterior-ventral margins converge at about 30° in the type species but at a much greater angle, about 150°, in *B. angulata*, suggesting attachment of the latter to harder and more planar substrates. The adductor muscles are somewhat anisomyarian with the anterior one varying from rather small to somewhat reduced. We have only observed the posterior adductor in *B. angulata*; it is medium-sized and rounded, and set close below the distal end of the escutcheon.

REMARKS. *Bowlandia* gen. nov. differs from *Goniophora* Phillips, 1848, in having a thicker shell, a more substantial hinge, and a sharp carinate, elongate escutcheon. It does not have the wide flange delimiting the posterior dorsal area that is present in *Goniophora*, nor the thin diverging internal buttresses that occur behind the umbones of that genus. It is most likely that the two genera belong to different superfamilies. *Goniophora* has recently been under investigation by Dr John Pojeta jr and may not be correctly placed in the Modiomorphidae. There are also no characters yet observed that link *Goniophora* conclusively with the Anomalodesmata.

Hind (1899: 338) proposed the name *Mytilomorpha* as a replacement name for *Goniophora* Phillips, 1848, because *Goniophorus* had been used by Agassiz for a genus of crinoids. This was, however, unnecessary. From Hind's statement *Cypricardia cymbiformis* J. de C. Sowerby is to be regarded as the type species of both *Goniophora* and *Mytilomorpha*, and therefore *Mytilomorpha* is an objective synonym of *Goniophora*.

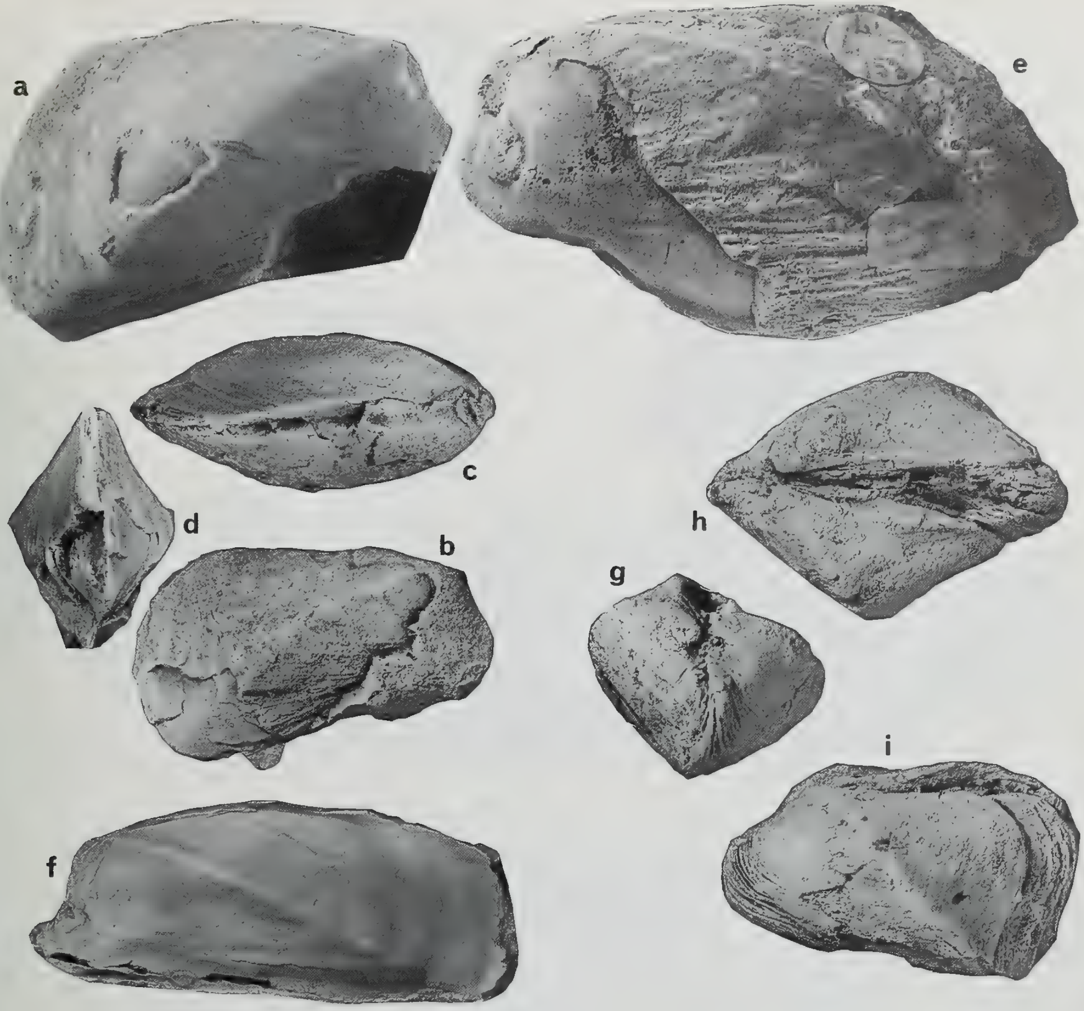
We consider that the Carboniferous species *Bowlandia rhombea* (Phillips) and *B. angulata* (Hind) should not be placed in *Goniophora*, and belong in fact to the Permophoridae. The similarity is superficial: where *Goniophora cymbiformis* occurs in a badly crushed condition, as in the Upper Silurian of the Ludlow area, it often occurs with a second, apparently unnamed species of similar size and shape but without the considerable flange, which is probably correctly placed in *Cosmogoniophorina* Isberg, 1934. The two have been sometimes thought to be the same species, but in our opinion, this second, Upper Silurian species and the genus *Cosmogoniophorina* itself, belong to the family Permophoridae.

Bowlandia may prove to be closely related to the Upper Permian genus *Naiadopsis* Mendes, 1952 (Runnegar & Newell, 1971: 56–7, fig. 25) from the Parana Basin. *B. rhombea* also closely resembles '*Ivanovia*' *slovenica* Astafieva-Urbaitis (not *Ivanovia* of Dubrolyubova), which is, however, only known from two views of the right side. *Bowlandia slovenica* apparently has a slight flexure of the pallial line, just below the posterior adductor.

Bowlandia rhombea (Phillips, 1836) Figs 43a–h

1836 *Cypricardia rhombea* Phillips: 209; pl. 6, fig. 10.
1885 *Sanguinolites rhombea* (Phillips); de Koninck: pl. 15, fig. 28.
1899 *Mytilomorpha rhombea* (Phillips) Hind: 338; pl. 38, figs 6–11.

LECTOTYPE. BM L3480, here designated, is the specimen



ig. 43 *Bowlandia rhombea* (Phillips). Figs 43a–e, Lower Carboniferous, Viséan, Bolland, Yorkshire; Fig. 43a, BM L3480, Gilbertson Collection, lectotype, side view of right valve; Figs 43b–d, BM 97182, similar to the lectotype; Fig. 43b, right side; Fig. 43c, dorsal view; Fig. 43d, posterior view; all ×1·5; Fig. 43e, PL5010, probable paralectotype, Gilbertson Collection (no. 97a), view of left side; ×2. Fig. 43f, Lower Carboniferous, Viséan, Poolvash, Isle of Man; BM L47456, large elongate specimen, left side of steinkern; ×0·67. Figs 43g–i, Lower Carboniferous, Tournaisian, Tournai, Belgium; BM PL5011; Fig. 43g, anterior view; Fig. 43h, dorsal view; Fig. 43i, left valve; *c.* ×2.

gured by Phillips, from the Carboniferous Limestone, iséan, at Bolland, Yorkshire; Gilbertson collection.

ARALECTOTYPE. BM 97182, from the same horizon and cality as the lectotype. Three further specimens from olland in the Gilbertson Collection (no. 97a) are listed *Cypricardia glabrata* Phillips and therefore are unlikely be syntypes. (BM L24821–3, Gilbertson Catalogue no. 7, are three syntypes of the true *Cypricardinia glabrata*. hey are clearly not the same as those of no. 97a; although etails of the hinge are not shown, they may belong to *leurophorella*).

THER MATERIAL. We refer the following specimens to *B. ombea*:

ind Collection: BM L45931–4, Castleton, Derbyshire; BM L45935–7, Elbolten, Yorkshire; BM L47451, Wetton Hill, Leek, Staffordshire; BM L47452–4 and BM L47456, Poolvash, Isle of Man.

Roscoe Collection: BM L43647, Wetton Hill, Leek, Staffordshire; BM L43616–26 and BM L43648, Narrowdale, Hartington, Derbyshire.

Butler Collection: BM L8175, Wetton Hill, Leek, Staffordshire.

Bather Collection: one specimen, Viséan, D_2, Peakhill Farm, Mam Tor, Derbyshire.

OTHER POSSIBLE SYNONYMS. De Koninck (1885) figured many specimens from the Carboniferous of Belgium under many new specific names. All were attributed to *Sanguinolites*, and most are closely similar to *Bowlandia rhombea*, though at the small sizes of most of them it is difficult to distinguish *Bowlandia* from the more carinate species of *Pleurophorella*. The following de Koninck species from the Viséan, étage 3, mostly from Visé, are probably synonyms of *Bowlandia rhombea: Sanguinolites apertus* de Koninck (1885: pl. 15, figs 1, 2), *S. solitarius* (pl. 15, figs 16, 17), *S. vexillum* (pl. 15, figs 19, 31, 32), *S. reversus* (pl. 15, fig. 25), *S. bipartitus* (pl. 15,

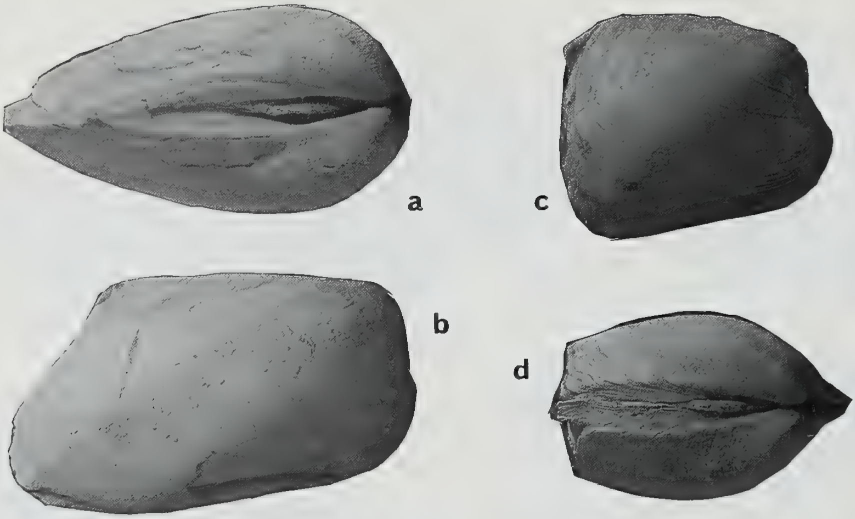


Fig. 44 *Bowlandia* sp. Figs 44a–b, Upper Carboniferous, Pennsylvanian, Missouri Series, Ochelata Group, Wann Formation; old uncompleted railroad cutting, 4 miles north and 2 miles east of Copan, Oklahoma, USA; USNM 6832, Conlin Collection; Fig. 44a, dorsal view; Fig. 44b, right valve. Figs 44c–d, Upper Carboniferous, Pennsylvanian, Canyon Series, Graford Group Shale, above Willow Point Island Member; Bridgeport Clay Pit, Wise County, Texas; USNM 7277, Conlin Collection; Fig. 44c, right valve; Fig. 44d, dorsal view. All slightly enlarged.

fig. 27), *S. quadricostatus* (pl. 15, fig. 34) and *S. reniformis* (pl. 15, figs 45, 46). The first specimen of *S. apertus* (pl. 15, figs 1, 2) is identical to *Bowlandia rhombea* except for the small rounded anterior gape which may have been for a byssus, but a second specimen (de Koninck, 1885: pl. 15, figs 3, 4) is much more elongate and may belong to a separate species. Other specimens from the same horizon and locality figured by de Koninck, but with de Rykholt specific names, that are probably also examples of *Bowlandia rhombea* are: *S. fabalis* (pl. 15, fig. 35), *S. praesectus* (pl. 15, fig. 37), *S. scapha* (pl. 15, fig. 38), *S. lyellianus* (pl. 15, fig. 39) and *S. tabulatus* (pl. 15, figs 41–4). Five more de Koninck (1885) species from other horizons and localities in Belgium that are probably also synonyms of *Bowlandia rhombea* are: *S. cuneatus* (pl. 16, figs 14, 15), *S. constrictus* (pl. 16, fig. 17), *S. angulatus* (pl. 16, fig. 18), *S. deletus* (pl. 16, fig. 19), all from étage 2, and *S. parvulus* (pl. 16, figs 20–3) from the Tournaisian.

COMPARISONS. *B. rhombea* is intermediate in form between *Permophorus* and *B. angulata* (Hind); the carina separates the flank from the posterior dorsal area at an angle of about 110° in *B. rhombea* but at only about 90° in *B. angulata*. The latter species, only recorded from the Viséan of Thorpe Cloud, Derbyshire, is also very much larger in all known examples except one, and has no trace of the radial cord on the posterior dorsal area close above the carina which is usually visible in *B. rhombea*.

Genus ***SILIQUIMYA*** nov.

TYPE SPECIES. *Sanguinolaria plicata* Portlock, 1843.

DESCRIPTION. Elongate, narrow genus of a similar shape to the Recent Solenacea genera *Siliqua* and *Cultellus*. Umbones well towards the anterior, shell thin with a slightly backwards-sloping sulcus in young growth stages only. The ligament and nymphs start between the umbones; they are opisthodetic and parivincular, long and straight. The dorsal margins are in juxtaposition from the umbones to the posterior margins. The nymphs are narrow and elongate with a narrow ligament groove. The ligament is set in a long, narrow escutcheon limited by sharp carinae.

The shell has a posterior inner rib at a very low angle to the hinge, which appears as a sulcus on the steinkern. The shell surface has low, rounded, comarginal rugae with no clearly defined corselet, although the rugae become irregular between the siphonal margins and the umbones. No surface pustules have been observed. The pallial line is very faint except close to the anterior adductor. The specimen illustrated in Fig. 45a has a relatively small, rounded and very faint posterior adductor scar and has been interpreted by Hind as having an entire pallial line; it is almost impossible to see the posterior part of the pallial line in a number of very well-preserved specimens, but none has a visible pallial sinus. The anterior adductor scar is rounded and slightly truncated towards the umbones. It is well inserted in front of a moderately thick buttress. There is a prominently inserted anterior pedal retractor between the anterior adductor and the umbones, lying close to the hinge. Small accessory muscle scars form a group of short incised striae on the anterior surface of the umbones of the steinkern. The shell appears to have a slight posterior gape (but see Hind, 1900: 389).

DISCUSSION. From M'Coy to the present time, *Siliquimya plicata* has always been placed in *Sanguinolites*. It differs from that genus, however, in having a more gently rounded posterior margin with no clearly defined corselet and in being less gibbous. It resembles a much elongated version of the Devonian genus *Glossites*. We have been influenced by the outline shape of ?*Pleurophorella striata* (Hind, 1900, 401–2; pl. 46, figs 1–2, & pl. 50, fig. 22), intermediate between *Siliquimya* and *Pleurophorella* of the Permophoridae. This leads us to suggest that *Siliquimya* should be included in the Permophoridae and its similarity to taxa included in the

Sanguinolitinae is partly a result of parallelism. Unfortunately the detailed characters of the accessory musculature of ?*Pleurophorella striata* that might corroborate this interpretation are as yet unknown.

Siliquimya plicata (Portlock, 1843) Figs 45a–c

?1842 *Sanguinolaria plicata* M'Coy, *in* Griffith: 12. *nomen nudum.*
1843 *Sanguinolaria plicata* Portlock: 433; pl. 34, fig. 18.
1843 *Sanguinolaria transversa* Portlock: pl. 34, fig. 21 [see discussion of *Wilkingia*, p. 73]
1844 *Sanguinolites plicatus* (Portlock); M'Coy *in* Griffith: 49; pl. 10, figs 3a, 3b.
1844 *Sanguinolites iridinoides* M'Coy *in* Griffith: 49; pl. 12, fig. 1.
1849 *Pholadomya iridinoides* (M'Coy); d'Orbigny: 128.
1900 *Sanguinolites plicatus* (Portlock); Hind: 387–8; pl. 44, figs 9, 11–15; pl. 45, figs 1–4.
?1900 *Sanguinolites striatus* Hind: 401; pl. 50, fig. 22 only.
[Fuller synonymies were given by Hind (1900: 387–8) and Paul (1941)].

TYPE MATERIAL. The holotype in the BGS collections, figured by Hind (1900: pl. 44, fig. 11), is a young individual with both valves preserved. The holotype of *Sanguinolaria transversa* Portlock, in the same collection, was also figured by Hind (1900: pl. 45, fig. 1). SM E1045, here designated the lectotype of *Sanguinolites iridinoides* M'Coy, is the specimen figured by M'Coy, and is from the Viséan of Lowick, Northumberland.

OTHER MATERIAL. BM PL2760, from the Viséan near Keswick, Northumberland. BM L5224, BM L28181–8, BM L46457 and BM L46473–6 from the Redesdale Ironstone,

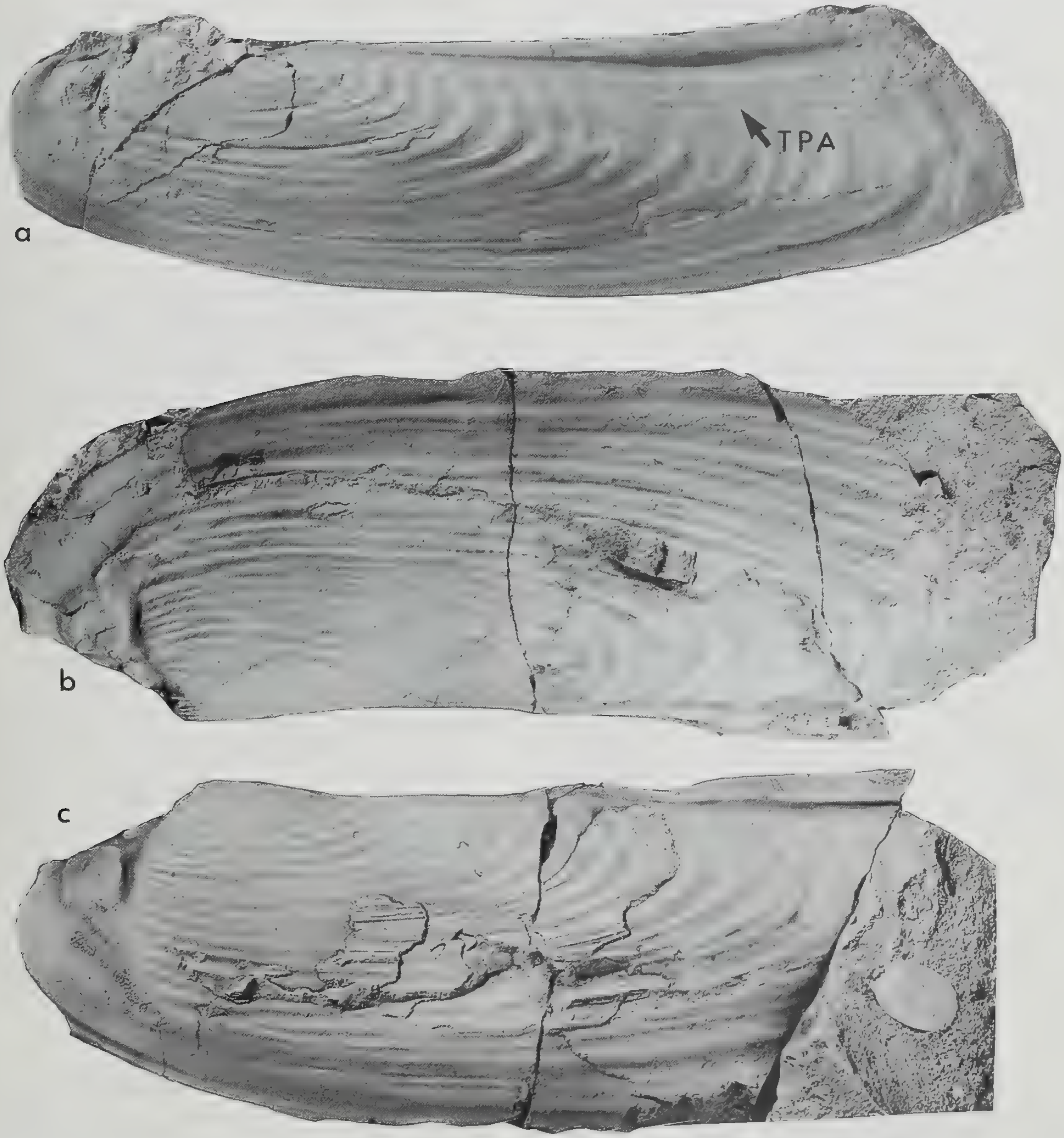


Fig. 45 *Siliquimya plicata* (Portlock). Upper Viséan. Fig. 45a, Lowick, Northumberland; SM E2817, left side, trace of posterior adductor clearly visible (TPA). Figs 45b–c, near Keswick, Cumbria; BM PL2760; Fig. 45b, right side of steinkern; Fig. 45c, left side. All ×1.

Asbian, of Redesdale, Northumberland. BM L8988 from the Viséan, Wardle Shale, near Edinburgh. BM L47507 from the Viséan, Upper Limestone, at Orchard, near Glasgow. BM L46479 from the Viséan, at Lawston Linn, Liddet Water. SM E2816–7, E20863 and E1046 from Lowick, Northumberland.

DESCRIPTION. An elongate, compressed, soleniform species with low umbones well towards the anterior. The anterior margins are subrounded and the posterior margins are obliquely truncated, sloping backwards, and form an angle with the dorsal margins, but are rounded ventrally. Some Redesdale Ironstone specimens have the shell preserved, apparently without periostracal spicules. The ornament consists of comarginal rugae which are offset and broader along a line between the umbo and the posterior ventral margin. The ligament is posterior, set on a long slender nymph. The dorsal margins are linear and contiguous to the posterior margin. The ligament is set down in a long, narrow carinate escutcheon; the carinae are sharp and very gently concave. The anterior adductors are subcircular and relatively small with a considerable thickening of the shell behind them in the form of a low, straight, slightly anterior sloping clavicle. The posterior adductors are hardly visible in most specimens; they lie well towards the posterior margin and close to the dorsum; they are subcircular. The pallial line is moderately incised at the anterior, but it is very difficult to follow towards the posterior. Hind (1900: 388) interpreted it, apparently correctly, as entire.

INCERTAE SEDIS

Genus *SPHENOTUS* Hall, 1885

TYPE SPECIES. *Sphenotus arcaeformis* (Hall & Whitfield, 1869), subsequently designated by Miller, 1889: 513, Middle Devonian, Hamilton, New York State. For a figure see Hall, 1885: pl. 65, figs 7–11. There are no modern illustrations of this species.

The generic name *Sphenotus* has been used by Driscoll (1965) and Pojeta (1969) for species we would include in *Pleurophorella*. Neither author based his opinion on a reconsideration of Hall & Whitfield's type species, which is of Middle Devonian age. Examination of Hall's illustrations suggests that these may be related genera but we do not find sufficient similarity to accept their synonymy. McAlester's Upper Devonian *Sphenotus tiogenesis* may be a thin-shelled mud-dwelling member of this genus (McAlester, 1962: 62; pl. 26, figs 1–14).

Genus **GRAMMYSIOIDEA** Williams & Breger, 1916

(See Runnegar, 1974: 931)

TYPE SPECIES. *G. princiana* Williams & Breger 1916: 133. from the Lower Devonian. Moose River. Miss. We have examined a syntype, USNM 66190, kindly lent by Mr F. Collier, which is badly crushed and distorted, and has no ornament preserved. This species was apparently quite wrongly illustrated in the *Treatise* (Newell 1969: N821). We conclude that at present the species and genus is unrecognizable and should be rejected as a *nomen dubium*.

A CLASSIFICATION OF THE ANOMALODESMATA

This study of Upper Palaeozoic Anomalodesmata has revealed a greater diversity than we previously suspected. It is the documentation of this diversity which we consider furnishes further information for the overall classification of the Anomalodesmata. Below we offer an interim classification of Upper Palaeozoic taxa which is a modification of Cox *et al.* (1969). Runnegar (1974) and Morton (1982). We expect to modify the classification further, when we study the Mesozoic taxa.

Subclass **ANOMALODESMATA** Dall, 1889

We interpret the characters of primitive members to include an aragonitic nacreoprismatic shell with periostracal spicules developed early in their history. The hinge consists of a slender hinge plate with an opisthodetic parivincular ligament set on slender nymphs and few or no hinge teeth. An escutcheon is usually present and the posterior dorsal margins are close and joined by periostracum. Adductors subequal to anisomyarian. Pallial line primitively without sinus. Shapes typical of sessile deep burrowers to byssate nestlers.

?Order **ORTHONOTOIDA** Pojeta, 1978

Superfamily **ORTHONOTACEA** Miller, 1877

[nom. trans. Pojeta, 1978]

Family **ORTHONOTIDAE** Miller, 1877

Elongate shells, apparently without periostracal spicules. Ligament external, opisthodetic.

Orthonota Conrad, 1841.
Palaeosolen Hall, 1885; gross shell characters convergent with the heterodont superfamily Solenacea.
?*Cymatonota* Ulrich, 1893.

Superfamily uncertain

Family **SOLENOMORPHIDAE** Paul, 1941

(=Solenopsidae Neumayr, 1883)

Elongate shells, with external opisthodetic ligament. Shell structure unknown. (The species *Solenomorpha elegantissima* Hayasaka, 1925 which has well preserved periostracal spicules has been better placed in *Alula* by Hayami & Kase 1977). An alternative classification would relate *Solenomorpha* to the elongate M. Devonian Sanguinolitinae with the lack of periostracal spicules interpreted as secondary loss. In that case Solenomorphidae would be closer to the mainstream anomalodesmatids.

Subfamily **SOLENOMORPHINAE** Paul, 1941

[nom. trans. herein]

Umbones towards or at the anterior. Deeper burrowing attained by elongation of the posterior shell.

Solenomorpha Cockerell, 1903; no spicules known.
Ennirostra Hajkr, Lukasova, Ruzicka & Rehor, 1975.

?Subfamily **PROMACRINAE** nov.

Radiating striae present, apparently without spicules. Elongation of shell anterior to umbones to give a *Donax*- or *Solemya*-like shape. Shell structure unknown, muscle scars poorly known.

Promacrus Meek, 1871.

?Family **PROTHYRIDAE** Miller, 1889

Dorsal part of anterior margins bear small protrusion.

Prothyris Meek (*in* Meek & Worthen 1869); fine radiating striae, no periostracal spicules.
Paraprothyris Clarke, 1913.
Amphikoilum Novozilov, 1956.

Order **PHOLADOMYOIDA** Newell, 1965

(?=Myoida Stoliczka, 1870;
=Desmodontida Neumayr, 1883)

Usually infaunal nestlers to very deep burrowers. Ligament primitively external, opisthodetic, becoming internal in several unrelated post-Palaeozoic lineages. Pallial line primitively without sinus, but developing this feature in several eparate lineages, the most advanced forms in this respect having long siphons of type 'C'. Shell surface bearing periostracal spicules in the primitive forms. Ordovician to Recent. A paraphylum including the ancestors of at least some septibranchs.

?Superfamily **EDMONDIACEA** King, 1850

Without surface spicules, buttressing parallel to hinge commonly present, characteristic pedal muscle scar pattern commonly present. Shell structure unknown. The Edmondiacea share shell shape and simplicity of hinge with the more primitive Pholadomyoida, characters which cannot be counted as firm synapomorphies. They do not possess the hypertrophied anterior adductor muscle, a synapomorphy of the Lucinoida, and it would be unreasonable to suggest that *Allorisma* had an anterior inhalent current which we would interpret as a primitive character possessed by most Lucinoida. Any arrangement of hinge teeth is more simple than that possessed by any of the major groups of Heteroconchia, so the Edmondiacea remain in the Pholadomyoida rather by default than by sharing any recognized synapomorphy.

Family **EDMONDIIDAE** King, 1850

(?=Cardiomorphidae Miller, 1877;
=Allorismidae Astafieva-Urbaitis, 1964)

Edmondia de Koninck, 1841.
Allorisma King, 1844.
Scaldia de Ryckholt, 1847.
Cardiomorpha de Koninck, 1841.

Family **MEGADESMIDAE** Vokes, 1967

(=Pachydomidae Fischer, 1886, nom. inval.)

Megadesmus J. de C. Sowerby, 1839.
Astartila Dana, 1847.
Pyramus Dana, 1847.
Plesiocyprinella Holdhaus, 1918.
Farrazia Cowper Reed, 1932.
?*Casterella* Mendes, 1952.

Superfamily **PHOLADOMYACEA** King, 1844

[nom. trans. Newell, 1965]
(=Grammysiacea Miller, 1877, nom. trans. Dickins, 1963)

Primitively myiform with external, posterior parivincular ligament mounted on paired upward-facing nymphs. Primitive shell structure considered to be nacreo-prismatic aragonite with radiating rows of periostracal spicules. Hinge line with few or no hinge teeth. Usually elongate shells with rounded or subrounded ends, often with a subumbonal sulcus. Shallow to deep sessile burrowers. Although a pallial sinus is present in many Upper Palaeozoic taxa, the more primitive lack this feature. We may interpret from this that they were primitively without siphons, but siphons of varying complexity, types 'B' or 'C', apparently develop separately in a number of lineages. The more primitive living forms are eulamellibranch filter feeders. A paraphylum including the Pholadomyidae and their Palaeozoic ancestors, together with the ancestors of the Thraciacea, Pandoracea, Poromyacea, Hiatellacea, Gastrochaenacea, Pholadidacea, Clavagellacea and probably the Myacea.

Family **GRAMMYSIIDAE** Miller, 1877

Sulcate forms with a break in shell ornament, becoming arcticiform. Ligament external, born on narrow nymphs. Shell structure unknown but surface commonly with radiating lines of periostracal spicules.

Subfamily **GRAMMYSIINAE** Miller, 1877

[nom. trans. herein]

Later taxa arcticiform, pallial line without sinus. Sulcus usually present.

Grammysia de Verneuil, 1847.

Subfamily **CUNEAMYINAE** nov.

Elongate, myiform, pallial line incompletely known. Shallow subumbonal sulcus sometimes present.

Cuneamya Hall & Whitfield, 1875.
?*Rhytimya* Ulrich, 1884.
?*Grammysioidea* Williams & Breger, 1916.
?*Protomya* Hall, 1885 (=*Palaeomya* Hall, *non* Zittel & Goubert, 1861).

Family **SINODORIDAE** Projeta & Zhang, 1984

[Elevated to a superfamily by Pojeta, Zhang & Yang, 1986.]

Sinodora Pojeta & Zhang, 1984.
Palaeodora Fleming, 1957.

Family **SANGUINOLITIDAE** Miller, 1877

Pallial sinus absent to deep. Ligament external opisthodetic, mounted on nymphs. Non-gaping to widely gaping. Hinge teeth usually absent but 'cardinals' known to be present in Alulinae. Nacreo-prismatic shell structure known in some sanguinolitines, probably occurred throughout the family.

Subfamily **SANGUINOLITINAE** Miller, 1877
(?=Arcomyidae Fischer, 1886)

Pallial sinus shallow or absent. Shell elongate. No hinge teeth.

Sanguinolites M'Coy, 1844.
Myofossa Waterhouse, 1969*b*.
Palaeocorbula Cowper Reed, 1932.
Ragozinia Muromzeva, 1984.
Cosmomya Holdhaus, 1913.
Grammysiopsis Chernychev, 1950.
Pentagrammysia Chernychev, 1950.
?*Siphogrammysia* Chernychev, 1950.
?*Glossites* Hall, 1885.
Cimitaria Hall & Whitfield, 1875.
Gilbertsonia gen. nov. (see p. 70).
?*Pachymyonia* Dun, 1932.
?*Leinzia* Mendes, 1949.

Subfamily **PHOLADELLINAE** Miller, 1887

Radial ribbing present.

Pholadella Hall & Whitfield, 1869.

Subfamily **ALULINAE** Mailleux, 1937

Median tooth present in RV only. Deeper burrowing attained by elongation of the posterior shell, convergent with Solenomorphidae.

Alula Girty, 1912.
Unklesbyella Hoare, Sturgeon & Kindt, 1979.
?*Tellinomorpha* de Koninck, 1885.

Subfamily **UNDULOMYINAE** Astafieva-Urbaitis, 1973

Deep pallial sinus known in some genera. Narrow anterior and or posterior gape sometimes present.

Wilkingia Wilson, 1959.
Praeundulomya Dickins, 1957.
?*Manankovia* Astafieva-Urbaitis, 1984.
Undulomya Fletcher, 1946.
Exochorhynchus Meek & Hayden, 1865.

Subfamily **CHAENOMYINAE** Waterhouse, 1966

Pallial line truncated by broad shallow sinus parallel to the vertical posterior margins; posterior gape wide and rounded.

Chaenomya Meek, 1865.

Subfamily **VACUNELLINAE** Astafieva-Urbaitis, 1973

Pallial line usually truncated with shallow to medium pallial sinus. Narrow posterior gape often present.

Vacunella Waterhouse, 1965.
?*Australomya* Runnegar, 1969.
Myonia Dana, 1847.

Family **PERMOPHORIDAE** van de Poel, 1959
[*nom. nov. pro* Pleurophoridae Dall, 1895]
(?=Kalenteriidae but not including Redoniidae Babin, 1966)

Elongate ovate of modioliform with external opisthodetic ligament usually mounted on narrow nymphs. Periostracal spicules present only in the more primitive forms. Usually not gaping. Cross-lamellar shell structure known in Jurassic taxa.

Subfamily **PERMOPHORINAE** van de Poel, 1959

Permophorus Chavan, 1954.
Pleurophorella Girty, 1904.
?*Pleurophorina* Licharew, 1925.
Siliquimya gen. nov. (see p. 90).
Bowlandia gen. nov. (see p. 88).
Ivanovia Astafieva-Urbaitis, 1978.
?*Cosmogoniophorina* Isberg, 1934.
?*Cosmogoniophora* McLearn, 1918.
?*Goniophorina* Isberg, 1934.
?*Naiadopsis* Mendes, 1952.
?*Jacquesia* Mendes, 1944.
?*Macackia* Mendes, 1954.
?*Roxoa* Mendes, 1952.

Other genera as listed in the *Treatise*, except for *Redonia* Rouault, 1851 which is unlikely to belong to the Anomalodesmata or the Heteroconchia.

Eager, 1978, discussed the evolutionary origins of the Anthracosiacae. His hypothesis included an ancestor for that superfamily among late Viséan, apparently marine taxa, which he called *Sanguinolites* Hind, *non* M'Coy. He specifically mentioned two taxa, *Sanguinolites abdenensis* and *Sanguinolites ovalis*. These species, described by Hind (1900), are not well preserved and details of their hinge and musculature are not fully known. One possibility is that they belong to *Pleurophorella* as interpreted in the present work (p. 84); in which case the Anthracosiacea could prove to be a non-marine offshoot of the Permophoridae.

NOMEN DUBIUM

Sphenotus Hall, 1885.

CONCLUSIONS

The Anomalodesmata were more prominent during the Upper Palaeozoic than in almost any modern environment, forming more than half of the total infaunal species in the British Viséan for example. However, they have slowly increased in numbers of species from the late Palaeozoic to the Recent. Their less prominent position today is purely the result of much more rapid diversification of other infaunal groups in the later Mesozoic and Tertiary, particularly the siphonate heterodonts.

Diagnosis of the subclass is difficult; it is recognized by particularly negative characters which include few or no hinge teeth and a generalized myiform shell. The parivincular ligament borne on nymphs, clearly primitive for the group, is shared by the Heteroconchia and the more primitive nuculoids. We recognize periostacal spicules as a primitive character for the mainstream Anomalodesmata that include the Pholadomyoida. This leaves us with considerable uncertainty as to which bivalves are the closest sister groups of this order.

The traditional inclusion of the Edmondiacea within the subclass and the disputed inclusion of the Orthonotida are neither confirmed nor denied by any evidence we have been able to find. The superficial resemblance between *Allorisma* (Edmondiacea) and the Undulomyinae is shown to be a case of convergence.

Our classification has made use of more taxa at the family and subfamily level than some recent classifications of this group, e.g. Newell, 1969 and Runnegar, 1974. Although the Upper Palaeozoic anomalodesmatids did not exploit the variety of internal hinges typical of the Mesozoic and Kainozoic, their diversity of shell shape and pallial sinus, both reflecting their life habits and our interpretation of their phyletic relationships necessitate this action.

The Upper Palaeozoic subfamilies within the Sanguinolitidae differ essentially from the non-siphonate Grammysiidae, particularly including *Grammysia* itself, in all developing deeper burrowing siphonate forms. We have been able to establish polarity of characters of the dorsal shell margins and hinge within the Sanguinolitidae. We have related this to the evolution of siphons. We have interpreted an elongate carinate escutcheon and no posterior gape as primitive and loss of carinate escutcheon and acquisition of a posterior gape as advanced. This polarity has guided us in our taxonomic evaluation.

One interesting aspect of the Runnegar schematic view of anomalodesmatid evolution (1974: text-fig. 3) is that it shows absolutely no interruption at the Permo-Triassic boundary except for the demise of the Australasian taxon Megadesmidae. At this time we are uncertain whether or not the Megadesmidae may themselves be ancestral to at least some septibranchs. In the evidence as it is known, we can also show no distinct indication of an extinction event at this time but feel the record close to the boundary, and particularly in the early Triassic, is so poor that at present no reasonable interpretation can be made. The one possibility of an extinction at the family level at this time is the Edmondiidae, but we do not know whether the Mesozoic family Mactromyidae is similar because of common descent or because of convergence.

We have established the broad similarity between the Permophoridae and the Sanguinolitidae which we interpret as reflecting a close phyletic relationship. As byssate nestlers, crevice dwellers and at least one apparent cavicolous taxon, they foreshadow some of the habits of their post-Palaeozoic descendants, which we believe may include the Gastrochaenacea and *Hiatella*.

The present apparent poverty or patchiness of the Devonian record of Anomalodesmata leads to a number of uncertanties; e.g. we are unable to show whether or not the multiplicity of development of siphonate forms which is apparent by the Lower Carboniferous (Viséan) is a result of an earlier Carboniferous radiation with some convergence of shape to early Palaeozoic taxa or whether the individual clades, subfamilies in this study, have a more ancient history. The earlier Palaeozoic Subfamily Cuneamyinae includes taxa with similar shape to the Upper Palaeozoic siphonate ones but we have been unable to discover the nature of the pallial line, and hence presence or absence of siphons, in this early group, nor whether there were repeated parallel radiations producing convergent forms.

This is of particular importance in considering the tracing of their history from the Palaeozoic through to the Mesozoic. The schematic evolutionary tree outlined by Runnegar (1974) and repeated by Morton (1987) is an over-simplification and is replaced here by a classification that is both rather more complicated and less certain in some details. However, the essential aspect of shallow burrowers giving rise to deeper burrowers, which may be interpreted from a comparison of shell morphology, remains a key insight into their evolution. Our own classification is outlined above.

The stratigraphical distribution within the Upper Palaeozoic of anomalodesmatids has been used for correlation, particularly in the early Permian of eastern Australia. We find further stratigraphical value in the Sanguinolitidae, particularly those with prominent or discordant ornament. We are, however, perplexed by, and unable to resolve without further field collecting, the bivalve fauna from the Upper Palaeozoic shale sequence from Peru, described by Thomas (1928). This has a distinct Upper Artinskian aspect but is accompanied in the collections at Cambridge and in Thomas' description by Pennsylvanian ammonoids. The distinctive part of the fauna includes species of *Ragozinia, Undulomya* and *Exochorhynchus*. Does this represent an earlier occurrence of taxa in an as yet unrecognized southern bivalve province, or is it the result of the mixing of two faunas, possibly when they were collected?

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Bryozoans from north Wales; *Alveolinella praequoyi*
sp. nov. from Papua New Guinea

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The Mesozoic Chrysalidinidae (Foraminifera, Textulariacea) of the Middle East: the Redmond (Aramco) taxa and their relatives.

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Synopsis. The seventeen Jurassic species of Textulariacea which had been named by Redmond (1965), placed by him in his new genera *Riyadhella* and *Pseudomarssonella*, and which had been used by Aramco for biostratigraphy in Saudi Arabia, have been redescribed and are re-illustrated. They are initially quadriserial, and may retain a simple, interiomarginal aperture; these include the terminally triserial *Riyadhella* emended and *Riyadhoides* nov.; or retain quadriseriality throughout ontogeny (*Redmondoides* nov.). The last of these contains *Redmondoides lugeoni* (Septfontaine) (*Valvulina lugeoni* Septfontaine) which is emended, for which metatypes are illustrated, and which is now recorded throughout Tethys. *Pseudomarssonella* is now restricted to initially quadriserial forms which gain areal, cribrate accessory apertures but still lack internal pillars. The acquisition of internal pillars characterizes *Paravalvulina* Septfontaine, a genus which ranges up into the earliest Cretaceous with *P. arabica* (Henson). Primary types and topotypes of this species (which was called *Dukhania arabica* by Henson) are also re-illustrated and redescribed. All these taxa are referred to the new subfamily Paravalvulininae.

The primary types and topotypes of *Dukhania conica* Henson are initially triserial and are referred to the subfamily Chrysalidininae Neagu; they are terminally biserial (unlike the terminally triserial *Chrysalidina* d'Orbigny, for which topotypes are illustrated) and have internal pillars, unlike the immediately ancestral *Praechrysalidina* Luperto Sinni, which is now also described from the Middle East. The Chrysalidininae are not older than Cretaceous.

Both the Paravalvulininae and the Chrysalidininae are referred to the Chrysalidinidae Neagu. They both contain specimens in which the micritic microgranules of the calcareous wall become aligned (the tests become 'protocanaliculate') and may even be canaliculate. The taxonomic significance of canaliculi is discussed and it is concluded that the development of canaliculation is gradational, from an initially random pattern of calcareous microgranules (in 'calc-agglutinated' walls), that the canaliculi might develop at various late ontogenetic stages (when their biological function became advantageous), and that their presence or absence cannot always be used to define supraspecific differences.

The probable phylogenetic histories of the Chrysalidininae and the Paravalvulininae, and the biostratigraphic value of their genera, are discussed.

INTRODUCTION

Detailed biostratigraphic studies in Saudi Arabia began in 1933, when Standard Oil of California was granted the first concession to explore for petroleum. After 1937, there was additional active participation by the Texas Oil Company, and, in 1944, the joint exploration company, once called 'California Arabian Standard', was renamed 'Aramco' (Arabian American Oil Company). Other companies joined, but from 1976 the Saudi Arabian governmental share-holding became 100%, and Aramco became a service company for the state, which was the holder of the world's largest national petroleum reserves. Many of the biggest oil-fields (Abqaiq, Abu Hadriya, Ghawar and many others) were found to have rich pay-zones in Jurassic rocks, and the Middle and Upper Jurassic biostratigraphy of Saudi Arabia became increasingly important, even in the early years of exploration.

As Redmond (1965) reported, 'a surprisingly large number of undescribed foraminiferal genera and species appear in the Middle and Upper Jurassic of Saudi Arabia'. Aramco agreed to release some of the material, and Redmond (1965) published descriptions of seventeen new 'ataxophragmiid' species, which he referred to his newly proposed genera *Pseudomarssonella* and *Riyadhella,* obtained from these rocks. The type specimens of these taxa were all solid, entire, and virtually matrix-free, and came from friable sediments sampled in water wells, stratigraphic wells or exploration wells drilled by Aramco, rarely from outcrops. As a result, strict topotypes could not be obtained by micropalaeontologists not associated with Aramco. Unfortunately, the original descriptions were accompanied only by small optical photomicrographs (all at × 50 magnification) in which many taxonomically important features (such as nature of the aperture, chamber arrangement, wall structure, etc.) were obscure. No thin sections of any specimens were illustrated or even recorded, so internal structures, if any, were unknown. Also, it became very difficult, if not impossible, to compare these taxa with those found by other companies, elsewhere in the Middle East, in random thin sections of micritic limestones. Limestones such as these (e.g., the Araej, Musandam, Uweinat, etc.) constitute the mid and late Jurassic deposits in most of north-east coastal Arabia – i.e. in Qatar, the United Arab Emirates, Oman, etc. Consequently, although Redmond's new taxa were used stratigraphically by Aramco (Redmond 1965, Powers 1968), they were not recorded publicly by workers in other oil companies.

Earlier, F. R. S. Henson and his associates (A. H. Smout, H. V. Dunnington and others), working on the Mesozoic rocks of Qatar, Iraq, Iran and Palestine, had recovered 'verneuilinids' from the early and mid Cretaceous which were referred to the new genus *Dukhania* (Henson, 1948). Redmond (1965) made no mention of these taxa, even though they had close morphological similarities to those which he had, himself, described; for example, they were microgranular, had 'agglutinating' walls, high spires, triseriality or quadriseriality, apertures which could become cribrate, etc. The species referred to *Dukhania* possessed internal pillars, but as no sections of *Pseudomarssonella* (in particular) had been prepared by Redmond, their morphological differences were not wholly clear.

In later years, Septfontaine (1977, 1981, 1988), after studying Mesozoic limestones (in thin section) from southern Europe and adjacent areas, published extensively on the morphology, taxonomy and possible phylogeny of high-spired 'valvulinids'. These included new taxa with extensive internal pillaring (e.g. *Paravalvulina*, reminiscent of *Dukhania*); this time, no isolated, entire specimens were known, and their morphology had to be deduced entirely from their (random) thin sections.

Luperto Sinni (1979), from the early Cretaceous of the same region, described sections of her new microgranular, 'agglutinating' genus *Praechrysalidina*, which had no pillars but which did possess a high, triserial spire and an areal, cribrate aperture. For over a century, another, widely recorded triserial form, with a terminal, cribrate aperture but with internal pillars, had been the mid-Cretaceous *Chrysalidina* (d'Orbigny, 1839). A phylogenetic pattern was almost visible, but was far from clear.

A similar lack of clarity beset the Jurassic taxa which lacked cribrate apertures and which often had unknown internal structures. While *Riyadhella* (and perhaps some *Pseudomarssonella*) had simple, interiomarginal apertures, this was also believed to characterize the quadriserial-triserial *Eomarssonella* (Levina, 1972), known as solid specimens from the late Jurassic of western Siberia, and the 'triserial' '*Valvulina lugeoni*' (Septfontaine, 1977), known only as random thin sections from the late Middle Jurassic limestones of southern Europe. There were several other published taxa; all were of Jurassic–Cretaceous age and had distinct morphological resemblances.

In an attempt to clarify their descriptions, review their systematics, revise their nomenclature, explain their phylogeny and determine their value in biostratigraphy, the collections of primary types of the taxa published by Redmond (1965) and by Henson (1948) have been restudied. Where possible, paratypes of species of *Riyadhella* and *Pseudomarssonella* have been thin-sectioned, so that the internal structure of these taxa is now known. Topotypic thin sections of limestones with '*Valvulina*' *lugeoni* have also been studied. The information from the primary types of *Dukhania* and related taxa has been supplemented by that obtainable from other, previously unpublished specimens (including topotypes) in the Henson and associates collection, deposited in the British Museum (Natural History). Specimens collected from Oman (Simmons & Hart 1987, Smith *et al.* 1990) and from the United Arab Emirates (BP Exploration and the Abu Dhabi National Oil Company) have also yielded much information.

SPECIMEN DEPOSITORIES AND STUDY METHODS

The Redmond Collection of Aramco specimens is deposited n the American Museum of Natural History (Department of Fossil Invertebrates), New York, USA (abbreviated to AMNH in this paper). The holotype specimens of each taxon are individually numbered, but the paratype specimens of each taxon are curated together, being mounted in a single paratype slide for each taxon, and bear a common number; these paratypes have been distinguished, for illustration in his paper, by a letter appended to the curation number. Both holotypes and paratypes bear curation numbers which are prefixed 'FT-'; thus, a particular paratype may be labelled here as 'AMNH FT-1234A'.

The Redmond specimens which were not sectioned were imaged by the ISI 60A scanning electron microscope (SEM), using the Environmental Chamber and back-scattered electrons; they have not been coated in any way. The paratypes which were sectioned were first imaged by the Hitachi 2500 SEM, using secondary electrons, and were coated with gold-palladium.

All specimens which are deposited in the British Museum (Natural History), Department of Palaeontology, London (abbreviated to BMNH in this paper) are registered by numbers prefixed 'P'.

THE NATURE OF THE TEST WALL

The nature of the composition and structure of the walls of so-called 'agglutinated' foraminifera has recently been discussed by Bender (1989) and by Loeblich & Tappan (1989), amongst others, and the views expressed in these papers have been taken into account here; in particular, the former has published some illuminating SEM imagery. However, it is necessary to redefine the terms which will be used here and to explain, albeit briefly, the reasons for these redefinitions.

All the taxa redescribed in this paper possess walls which are dominantly or wholly calcareous (calcitic), which may or may not possess canaliculi (as discussed below) and which may or may not contain clearly inorganic, mineral fragments (such as fine silt quartz grains). In spite of the differences which can occur between them (such as, for example, the presence or absence of silt quartz), they are obviously all essentially the same: none has the characters which would lead to their recognition as being walls of Rotaliina, for example. We explain below how they are all easily recognizable as belonging to members of the Textulariina.

The walls of the Textulariina may be constructed of inorganic (originally terrigenous) grains, glued together by organic (mucopolysaccharide?) cements. Such walls occur particularly in benthonic species which inhabit (or inhabited) oceanic waters below the calcium carbonate compensation depth, or marsh environments of low pH, or other habitats where solid calcium carbonate could not survive. Elsewhere, the organic cements could be supplemented by secretion of calcium carbonate; analogously to the 'dry-stone walling' technique of humans, the gaps between the terrigenous mineral grains of the walls could be filled with packed microgranules of calcite. This calcite retains its microgranular form when viewed by SEM, showing that the microgranules are, themselves, coated with ultramicroscopically thin organic laminae – if they were not, the form of the microgranules would have been lost, and the calcite would have been visible as a continuous, undivided mass. The organic cements may be constructed of fibres, nets, 'foam' or sheets, or combinations of these (Fig. 1a). They 'glue' the terrigenous grains or calcitic microgranules together, to make a coherent, continuously structured wall; the term 'agglutinated' (from *glutinare*, to glue) is appropriate, whether the calcitic microgranules were secreted by the foraminifer or not; the term 'arenaceous' is most inappropriate, as no 'sand' grains may be involved. In fact, no inorganic grains of terrigenous, mineral origin may be present at all.

Some textularine taxa may have walls wholly composed of microgranules of calcite, agglutinated together (Bender 1989: pl. 8). These are 'agglutinating' but they are certainly not 'arenaceous'. These calcite microgranules may be arranged randomly in the walls, or they may be agglutinated into parallel rows, virtually or wholly perpendicular to the wall surface (Fig. 1b). In neither case is there any alignment of the optical axes (the 'c-axes') of the calcite microgranules; in thin section, the wall may have its more transparent

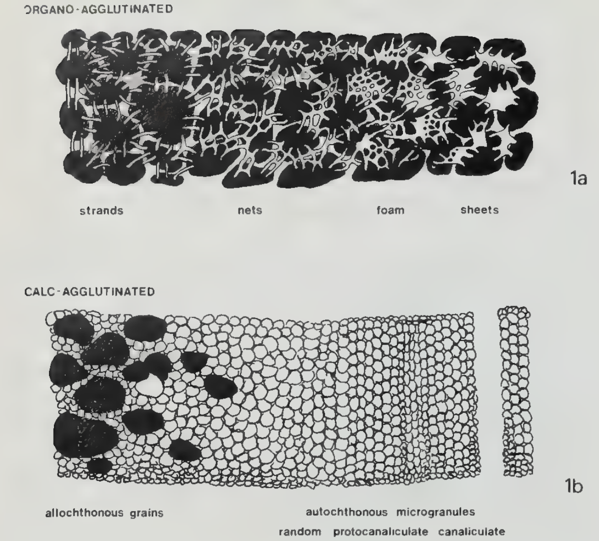


Fig. 1 The wall structures of members of the Textulariina: the black grains represent non-calcareous particles of rocks or minerals, while the white microgranules represent calcareous (calcite or aragonite) autochthonous particles.

a, the forms of *organo-agglutinated* cements: separate organic *strands* become joined to form *nets*, and these nets infill to form porous *'foam'* or non-porous *sheets*.

b, in *calc-agglutinated* tests, allochthonous foreign grains may be cemented together by calcareous *microgranules*; these autochthonous microgranules may remain randomly arranged but may build the wall in the absence of foreign, allochthonous grains; when the microgranules become arranged in parallel rows, perpendicular to the wall surface, the wall becomes *protocanaliculate*; canaliculi can develop between these parallel stacks of microgranules, so that the wall becomes *canaliculate*.

(lighter-coloured) zones, where the microgranules are larger, or its darker, less translucent zones, where the microgranules are smaller, but in no case has the wall a 'fibrous', 'glassy' or 'hyaline', rotaline appearance. In the latter, the optical axes of the aligned microgranules are themselves aligned, so that the parallel rows of microgranules, with their equally parallel c-axes, look like fibrous crystals when seen through an optical microscope. If the c-axes are orientated perpendicular to the wall surface, such 'hyaline' walls have been called 'radial', but if the c-axes of groups of aligned microgranules are oblique to the wall surface, with different directions of obliquity, then they have been called 'granular' (Loeblich & Tappan 1964: C94–95). This latter term was a reference to the optically 'granular' or 'speckled appearance of the surface ... in polarized light, owing to different grain orientations and resultant differences of refractive index. Some . . . forms may even appear granular in reflected light . . .'. (Loeblich & Tappan, *loc. cit.*). It is now clear that the use of the term 'granular' for this optically speckled appearance (e.g., as in Loeblich & Tappan, 1988: 615) must be abandoned for the sake of the consistently meaningful, morphological usage of the names 'granule' and 'microgranule'. All the forms of wall discussed above are morphologically microgranular when viewed by SEM; granules of minerals may be agglutinated into walls which have no optical, c-axis linearity. So we suggest that 'microgranules' be used to label grains which can only be distinguished by electron microscopy (e.g., by SEM), while 'granules' be reserved for grains which can be distinguished by optical microscopy.

Also, we suggest that the *agglutinated* taxa, in which the optical axes of constituent microgranular and/or granular minerals are randomly orientated and are not regularly aligned, may include

(a) taxa with organic cements only (these organic cements may, themselves, be fibrous, laminar or microgranular), and are *'organo-agglutinated'* (Fig. 1a);

(b) taxa with additional ferric or other non-calcareous microgranular cements (e.g. *'ferro-agglutinated'*);

(c) taxa with additional calcareous material (i.e. *'calc-agglutinated'*), maintained as microgranules by ultramicroscopic organic membranes; these calcareous microgranules may (as in the categories above) also agglutinate allochthonous grains of other minerals (e.g., quartz); also, the microgranules may be randomly packed or agglutinated into parallel rows, usually perpendicularly to the wall surface (Fig. 1b).

All of these categories belong to the Textulariina Delage & Hérouard, 1896 (see Loeblich & Tappan, 1988).

All the taxa in the Redmond, Henson and other collections described in this paper have walls in category (c); all are *calc-agglutinated microgranular*. Additionally, some may also agglutinate quartz granules, and some may be partly canaliculate. The significance of the latter is discussed below.

THE SIGNIFICANCE OF CANALICULI IN TAXONOMY

Canaliculi in classification

The presence or absence of canaliculi, in the walls of Textulariina with calcitic cement, has been used by Loeblich & Tappan (1988, 1989) as a morphocharacter to define the difference between superfamilies (e.g., canaliculate Textulariacea, noncanaliculate Verneuilinacea). However, it had already been pointed out (e.g., by Banner & Desai 1985, Desai & Banner 1987) that canaliculi evolved independently in different lineages, at different times in the Mesozoic and Palaeogene, and that the superfamilies could not be distinguished on one morphocharacter alone. Even some genera (e.g., canaliculate *Dorothia* developing from ancestral, noncanaliculate *Praedorothia*) could evolve more than once. The canaliculate descendants are superficially so similar to their noncanaliculate ancestors that they are generically indistinguishable unless they are sectioned, or broken and viewed with SEM; any useful classification would group them together, so that their identity could be immediately compared. To separate into different superfamilies the members of such closely related pairs of genera as *Praedorothia* – *Dorothia*, *Protomarssonella* – *Marssonella*, *Textulariopsis* – *Textularia*, *Pseudoclavulina* – *Clavulinopsis*, *Verneuilina* – *Hemlebenia*, *Gaudryina* – *Connemarella*, etc, when the different pairs are not closely related to the other pairs, would produce a suprageneric classification which would be misleading both phylogenetically and taxonomically. Clearly, for example, *Praedorothia* and *Dorothia*, both of which secrete calcitic cement, have the same coiling and growth modes, and the same apertural, test and chamber shapes, should be referred to the same superfamily (maybe even to the same family), even though one is canaliculate and one is not. One directly and repeatedly evolved from the other. Forms which are intermediate in this evolution, and in which the canaliculation of the wall was partial or indistinct, would produce great problems of classification if the supraspecific characters were to be artifically elevated into major, suprageneric ones.

Tubule-containing and canaliculate walls

Even when there is no known evolutionary transition from one category into another, lack of careful distinction of the nature of a textulariid wall can lead to confusion. An example is *Spirorutilis wrighti* (Silvestri). Banner & Pereira (1981), in their study of canaliculation in the textulariids, believed *S. wrighti* to have solid walls, and referred it to the solid-walled Spiroplectamminidae (in contrast to the canaliculate Textulariidae). Their SEM photographs of this species, and of its wall, were reproduced by Loeblich & Tappan (1988: pl. 120), who used its supposed senior generic synonym *Spiroplectinella* and placed it in the solid-walled Superfamily Spiroplectamminacea (1988: 110–112), far from the canaliculate Superfamily Textulariacea (1988: 168). This was followed by Hottinger *et al.* (1990). However, Bender (1989: 298; pl. 10, fig. 1; pl. 16, fig. 25) has shown that specimens of '*Spirorutilis*' *wrighti* have walls which are far from solid, even though she still places them in the Superfamily Spiroplectamminacea. She distinguishes (1989: 277) three types of 'porensysteme' within those textulariids which use calcite cement: the 'anastomosierende' (anastomosing, irregularly shaped, but often narrow and characteristically tubular) spaces in the walls of, e.g., *S. wrighti* (the type species of *Spiroplectinella* Kisel'man), and now also shown to be present in the walls of '*Textularia*' *carinata* d'Orbigny (the type species of *Spirorutilis* Hofker) by Hottinger *et al.* (1990); the 'geradlinig unverzweigt' (rectilinear, unbranched) canaliculi of *Textularia* spp.; and the 'distal verzweigt' (distally branched) canaliculi of *Valvulina*, *Clavulina* spp. and '*Gaudryina*' *rudis* (Wright), the last species used, because of its canaliculation, to typify the new genus *Connemarella* of the Textulariacea by Loeblich & Tappan, 1989. Clearly, distinction must be made between taxa which have walls with anastomosing, irregular tubules and those which have true, regular, subparallel canaliculi, even though the walls of neither are truly solid. The tubules are not known to evolve into canaliculi; the latter seem to have their origin in truly solid, calcitic walls in which the constituent granules become regularly aligned.

Protocanaliculate walls

It has been shown that in some species not known to have had canaliculi, the calcareous granules of their walls could become aligned in a way which would allow canaliculation readily to develop. The latter would have been able to develop 'between these vertical parallel stacks of granules' (Banner & Desai, 1985: 87, regarding *Verneuilina tricarinata* d'Orbigny, their pl. 3, figs 7, 8). We can term these calcitic, solid-walled species, in which the constituent granules are aligned in parallel rows perpendicular to the wall surface, 'proto-canaliculate'.

However, fully canaliculate species (even wholly calcareous ones) often do not readily show such alignment of granules even when the canaliculi, themselves, are prominent (e.g., *Valvulina oviedoiana* d'Orbigny, as figured by Banner & Pereira, 1981: pl. 9, figs 1–3, 8), but such alignment may, nevertheless, be present. Bender & Hemleben (1988) showed not only that the calcitic cement of *V. oviedoiana* was biologically secreted but that in it, also, the granules ('individual crystals') of calcite were aligned into granular rods (1988: pl. 1, figs 4, 6, 7), and that the granules and their rod-like assemblages were coated with 'organic envelopes' (1988: pl. 1, fig. 5). The rod-like parallel stacks of granules could themselves be grouped parallel to each other, to produce 'packets' of granules in parallel rows (Bender 1989: 276). These 'packets' of 'rods' of aligned calcitic granules, as seen between the canaliculi in Holocene *V. oviedoiana*, closely resemble those observed in some Cretaceous taxa (e.g., *Dorothia pupa* (Reuss), as figured by Desai & Banner, 1987: pl. 1, figs 2c, 2d).

The walls of some Mesozoic taxa (e.g., *Marssonella oxycona* (Reuss), as figured by Desai & Banner, 1985: pl. 3) have fibrous units of calcite aligned parallel to each other, and parallel to the canaliculi which are present between large groups of them. These fibrous units show no sign of granular composition, and they do not seem to be grouped into 'packets'. The canaliculi of *Marssonella* are separated by far greater numbers of fibrous units than the smaller numbers of granular 'rods' which constitute the walls between the canaliculi of *Dorothia* (see, e.g., Desai & Banner, 1985: pls 1–3). Such differences of structure may prove to be characteristic of different genera and separate evolutionary lineages, but more research must yet be undertaken.

Nevertheless, it seems clear that alignment of the primary calcitic constituent granules of the walls was necessary prior to the development of canaliculi. It has been assumed (e.g., by Banner & Desai, 1985) that such alignment may characterize species but cannot be used to distinguish supraspecific groups, in contrast to the presence of canaliculi, which can be used for such distinction; indeed, as noted above, Loeblich & Tappan (1988) used them to distinguish groups as important as superfamilies.

The ontogenetic appearance of canaliculi

Although it has never been explicit, the assumption has been made that such alignment of wall structures was constant throughout the ontogeny of the species concerned – that such alignment of primary calcitic granules or the presence of canaliculi appeared at a given stage of evolution, and thereafter occurred uniformly from nepionic to ephebic (and maybe even gerontic) growth stages. Certainly, in some figured taxa, canaliculi are uniformly present in the chamber walls throughout test growth; examples include Recent *Textularia agglutinans* d'Orbigny (e.g. Banner & Pereira, 1981: pl. 1, fig. 6) and Cretaceous *Dorothia pupa* (Reuss) (Desai & Banner, 1987: pl. 1, fig. 2b). The possibility that, in other taxa, there were ontogenetically late appearances and development of canaliculi was not considered.

The speed of evolution of canaliculi

The apparent uniformity of the appearance and development of canaliculation in the walls of some taxa could have resulted from the rapid evolution of canaliculi during the phylogeny; it could have been that canaliculi first developed in late ontogenetic stages, and later spread to earlier ones, but that in the fossil record this 'ontogenetic spread' is hidden by the rapidity of the evolution as a whole. The evolution would appear to have been 'punctuated', as in the phylogenetic appearance of the Textulariidae (as redefined by Banner & Pereira, 1981) or of true *Marssonella* (Desai & Banner 1987). In such cases, the presence or absence of canaliculi provide clear, biostratigraphically useful, supraspecific taxonomic distinctions.

In other cases (e.g., the *Chrysalidina* evolution studied here), the evolutionary acquisition of canaliculation was much slower, more 'gradual'. The late ontogenetic development of canaliculi was not hidden in an abbreviated fossil record. The development of canaliculi during test growth could have been entirely related to the acquisition of individual ontogenetic maturity, possibly under particular microenvironmental conditions, and was not acquired by all specimens at all of their growth stages, at a recognizable evolutionary point in their phylogenetic lineage – or even at identical ontogenetic points. In these cases, the presence or absence of canaliculi cannot be used for supraspecific taxonomic distinction, and cannot even be used, independently, to distinguish between species.

This exemplifies the rule which applies in the study of all groups of foraminifera: a particular morphocharacter may be of taxonomic importance and biostratigraphic usefulness in one group, but may be of little taxonomic utility and of limited biostratigraphic value in another, even closely related, group.

Canaliculi, keriothecae and alveolae

The variable taxonomic importance of the development of canaliculi has been accepted by, e.g., Septfontaine (1988), who diagnosed his concepts of the Mesoendothyridae as always possessing a 'keriotheca', the Hauraniidae in lacking it (but possessing a 'hypodermal network'), and the Valvulinidae as sometimes possessing it. The closely spaced and parallel canaliculi of many Lituolacea (e.g., in Mesozoic *Lituosepta* of the Mesoendothyridae (*sensu* Septfontaine, 1988; Orbitopsellidae *sensu* Loeblich & Tappan, 1988) and Cenozoic *Valvulina* of the Valvulinidae) produce a wall structure which morphologically closely resembles the keriotheca of many Palaeozoic fusulinids (e.g., the Schwagerinidae). When the canaliculi are thin-walled and very closely spaced, as in the paratype *Dukhania conica* Henson (Fig. 25a, p. 114), the resemblance to a schwagerine keriotheca is very strong. They may well have had an analogous biological function, but there can be no doubt that the structures were evolved independently, and have different taxonomic and biostratigraphic value in different foraminiferal groups.

Thicker-walled, more widely spaced canaliculi have strong resemblance to the structures called 'alveoli' in lituolids such as *Alveosepta*, *Buccicrenata*, *Alveocyclammina*, etc. (see illustrations in Loeblich & Tappan, 1988); these narrow hypodermal alveoli may branch, but, as Bender (1989, see above) has pointed out, so can the canaliculi of *Valvulina*, *Clavulina*, etc. (see, for example, the bifurcating canaliculi of *V. oviedoiana* d'Orbigny, figured by Banner & Pereira, 1981: pl. 9). The only morphological distinction between such broad canaliculi and narrow alveoli seems to be the internal closure of the former by pustulae of the inner organic lining of the wall (illustrated by transmission electron microscopy in Bender, 1989: pl. 10, figs 3–5), which are sometimes calcified and preserved even in fossils (illustrated by SEM in Banner & Pereira, 1981: pl. 6, fig. 6; pl. 8, fig. 8; pl. 9, fig. 11).

Again, there may well have been analogous biological functions for both structures. It has been suggested that the narrow hypodermal alveoles of *Alveosepta*, etc., which appear to have evolved in conditions of reduced illumination, could have allowed ionic exchange between internal cytoplasm and surrounding sea-water, through the extremely thin epidermis (Banner & Whittaker 1991); the canaliculi of the textulariids probably had, and probably still has, a similar function. This contrasts with the broad hypodermal alveoles of lituolids which inhabited very shallow, tropical water (e.g., *Pseudocyclammina lituus*); such species may have used the environmental irradiance for photosymbionts in the alveoli, a function which canaliculi could not have had (Banner & Whittaker 1991).

Summary and conclusions

The development of canaliculi during phylogenesis seems to have been to the biological advantage of the evolving taxa; they may well have aided the organism directly but subtly to control its cationic concentration. Canaliculi independently appeared in several lineages, and once gained they were never lost; there is no example of their evolutionary disappearance.

Canaliculi, narrow hypodermal alveoli and schwagerinid keriothecae could all have had analogous biological functions. However, they cannot be proved to be homologous; they certainly evolved quite independently. Morphological extremes of each are clearly distinguishable (the morphological similarities between the other extremes can be confused but do not indicate their identity), and they should be given separate names and definitions. Essentially, the keriotheca is a uniform mass of favosely arranged, parallel, narrow tubules, each thin-walled and much longer than it is broad, and all are closely appressed; the chamber wall (the keriotheca) *consists* of these tubules. In contrast, canaliculi penetrate the microgranular chamber wall, are not closely appressed, and are independently sealed by pustules of the inner organic lining. Alveoles are similarly spaced but have no such inner seal, and can be almost as broad as they are long (especially in lituolids with thin chamber walls).

Canaliculi appeared relatively abruptly in the evolution of some lineages but slowly in others. Even the protocanaliculate evolutionary stages can be recognized to have appeared slowly and independently. When canaliculi evolved slowly, they can be seen to have first appeared in the last growth stages of the tests. It was probably in that phase of life, when the test was largest, that the canaliculi were most useful in providing means (additional to those in the extruded pseudopodia) for the intracameral cytoplasm to communicate biochemically with exterior seawater. When species, such as those of *Dukhania* and *Chrysalidina*, develop with canaliculi only in the last chambers of some specimens, the use of canaliculi to define suprageneric differences (such as those between families and superfamilies) becomes impossible. It is unwise to attempt it even when the evolutionary acquisition of canaliculi is relatively abrupt, as it is then misleading both taxonomically and phylogenetically.

SYSTEMATIC PALAEONTOLOGY

Superfamily **TEXTULARIACEA** Ehrenberg, 1838

Family **CHRYSALIDINIDAE** Neagu, 1968

DIAGNOSIS EMENDED. Wall microgranular, agglutinating, calcareous, with relatively small amounts (if any) of agglutinated, oncalcareous grains, and solid (sometimes protocanalicuate) or canaliculate, or both; test high trochospiral, with uinqueserial or quadriserial or triserial or biserial coiling odes, or with certain consecutive pairs of these; the rimary aperture is interiomarginal and centred about the ong axis of coiling; in terminally quadriserial or quinqueerial forms, an umbilicus is present and the aperture is overed with a broad intraumbilical flap; the umbilical flap ay be penetrated by areal, multiple, pore-like, accessory pertures, and internal pillars may develop between successive intraumbilical flaps.

EMARKS. This family is divisible into two subfamilies, which ontain genera which may be morphologically very similar *Dukhania* of the Chrysalidininae, *Paravalvulina* of the Paraalvulininae) but which have different origins and give ultiate rise to morphologically very different forms. The Creaceous Chrysalidininae are essentially triserial, initially at east; they evolve as a single lineage, developing umbilically illared genera which are, successively, terminally biserial, hen triserial and ultimately quadriserial (or even multierial), as the internal zone of pillaring became increasingly road. In contrast, the mainly Jurassic Paravalvulininae Bajocian–Kimmeridgian, surviving into the Valanginian and ossibly the Hauterivian), are quinqueserial and/or quadrierial, or both, evolving forms which are terminally triserial; hese may be very slender (some species of *Riyadhoides* nd *Riyadhella*) or broadly conical and internally pillared *Paravalvulina*).

Subfamily **CHRYSALIDININAE** Neagu, *nom. transl.*

IAGNOSIS. Test triserial throughout ontogeny (at least in the egalospheric generation) or becoming biserial or quadrierial in the adult.

EY TO GENERA INCLUDED

.Triserial throughout, no internal pillars: *Praechrysalidina* Luperto Sinni, 1979 (Hauterivian?–Barremian–Albian)

. Initially triserial (in megalospheric form), with internal pillars:
- 2.1. Biserial in adult:
  - 2.1.1. Septa convex:
    - 2.1.1.1. Chambers relatively low, septa at broad angles to long axis of test: *Dukhania* Henson, 1948 (Aptian/Albian?–Cenomanian)
    - 2.1.1.2. Chambers relatively high, septa oblique to long axis of test: *Pseudochrysalidina* Cole, 1941 (Eocene)
  - 2.1.2. Septa plano-concave: *Vacuovalvulina* Hofker, 1966 (Palaeocene)
- 2.2. Triserial in adult: *Chrysalidina* d'Orbigny, 1839 (Aptian?–Cenomanian)
- 2.3. Quadriserial (or multiserial) in adult: *Accordiella* Farinacci, 1962 (Coniacian–Santonian)

EMARKS. *Vacuovalvulina* must have arisen independently rom the phylogeny described below, probably evolving from analiculate, true *Marssonella* at or near the Cretaceous–alaeogene boundary, but its evolution is not yet demonstrble; if this supposition is correct, then *Vacuovalvulina* does ot belong to the Chrysalidininae as here understood.

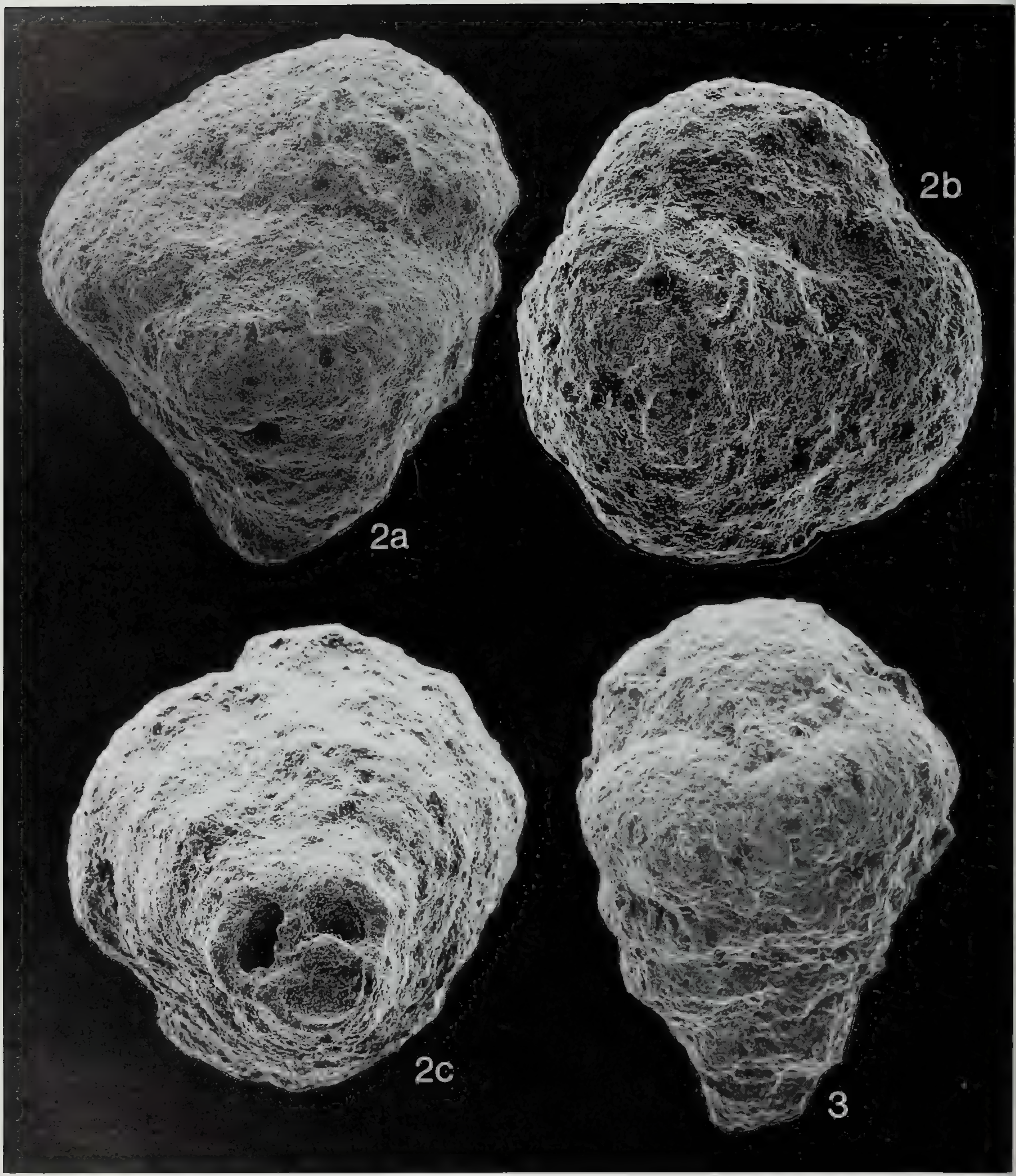
Pseudochrysalidina may also ultimately be removed from his subfamily, as it may have evolved directly from *Valvulina* but this, also, has yet to be demonstrated.

Genus ***PRAECHRYSALIDINA*** Luperto Sinni, 1979

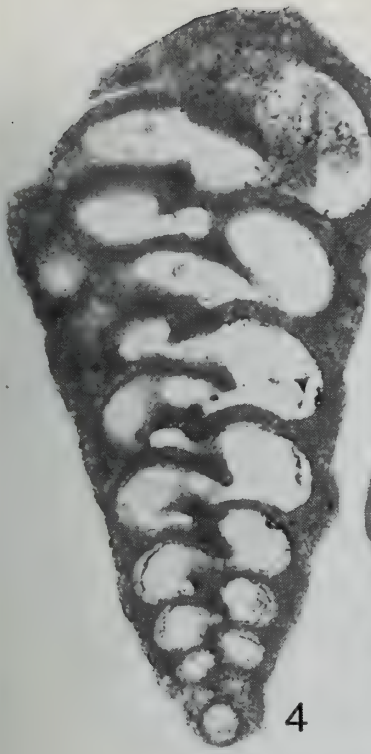
TYPE SPECIES. *Praechrysalidina infracretacea* Luperto Sinni, 1979 (see Figs 2–8).

REMARKS. In his synoptic, comprehensive study of Mesozoic neritic foraminifera, Septfontaine (1981: 184, 188) noted the appearance, in the early Cretaceous, of 'Valvulines spéciales' which he believed were descended from *'Valvulina' lugeoni* by developing modification to the 'dent valvulaire' analogous to that later displayed by *Chrysalidina*; he figured a random thin section of this form, showing its characteristic multiple, pore-like, areal apertures, from Lower Cretaceous limestone of Turkey (1981: pl. 2, fig. 12). Earlier, Gušić (1975: 26; pl.4) had figured the same species, from the 'Uppermost Aptian – Lowermost Albian' of Mt Medvednića, northern Croatia, Yugoslavia, as '*Chrysalidina* cf. *gradata* d'Orbigny'; he noted that this form lacked the pillars and buttresses of true, Cenomanian *Chrysalidina*, and should be distinguished. Both of these authors clearly recognized the affinity of these early Cretaceous forms to the late Cretaceous genus, and believed that they deserved recognition. In 1979, Luperto Sinni described and named it, using thin sections of specimens (from the limestone of the terminal part of the early Aptian of western Italy) as the primary types. Later (*in* Schroeder & Neumann 1985: 22) she recorded it also from the late Aptian and late Albian, and from localities as far afield as Somalia, suggesting that it might form part of an evolutionary lineage *'Valvulina' lugeoni → Praechrysalidina cretacea → Chrysalidina gradata → 'Chrysalidina' (vel Pseudochrysalidina) floridana*.

We believe that this phylogenetic theory must be modified. There is no evidence to link *Praechrysalidina infracretacea* with *'Valvulina' lugeoni* (here placed in *Redmondoides* n. gen., p. 125), and there is a considerable stratigraphic gap between them. Also, *P. infracretacea* is, like its descendants, initially triserial. We would refer it to the subfamily Chrysalidininae, separate and distinct from the stratigraphically earlier, fundamentally quadriserial Paravalvulininae. The stratigraphically oldest known occurrences of *P. infracretacea* are those recorded by Simmons & Hart (1987) from the Habshan Formation (probably Valanginian) of Oman. We suspect that *Praechrysalidina* arose quickly but directly from *Verneuilinoides* sp., in the earliest Cretaceous, by the opening of the umbilicus and the acquisition of broad apertural flaps, which rapidly became penetrated by accessory, areal, cribrate, pore-like apertures. In ontogeny, the interiomarginal primary aperture remained open in the nepionic growth stage, but in neanic growth this became covered by the perforated, broad, apertural plate-like flaps, while the accessory interiomarginal aperture still remained. By the ephebic stage of development, the flaps became fused to the terminal faces of juxtaposed chambers, and the accessory interiomarginal apertures became sealed. Only the areal accessory apertures remained open to allow the internal cytoplasm access to the exterior of the test. The primary interiomarginal apertures, now wholly internal, became high and wide, and occupied the whole height of what was once the apertural faces of the chambers. Consequently, the apertural flaps became convexly inflated (Figs 4–8), producing a convex termination to the tests (Figs 2–3), heralding the evolution of the succeeding *Dukhania* and *Chrysalidina*. The juxtaposed chambers separated in their axio-medial areas, and a true umbilicus developed, always covered by the apertural flaps.



Figs 2–3 *Praechrysalidina infracretacea* Luperto Sinni. Figs 2a–c, BMNH P 52580, from Qatar, well Dukhan-2, 4375–4380 ft depth. Hauterivian. a, axial view (length 1320 μm), × 70. b, terminal view, × 70. c, initial view, showing triseriality, × 70. Fig. 3, BMNH P 52581, from United Arab Emirates, well Umm Shaif-2, Upper Shuaiba Formation, Aptian; axial view (length 1180 μm), × 80.



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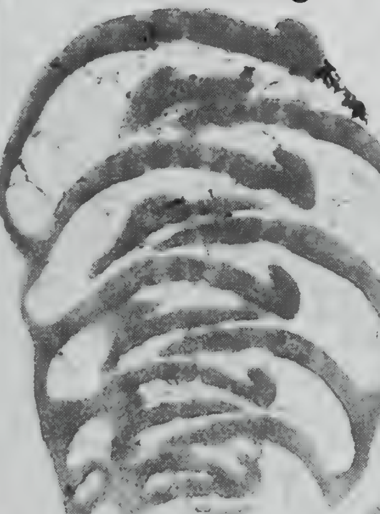

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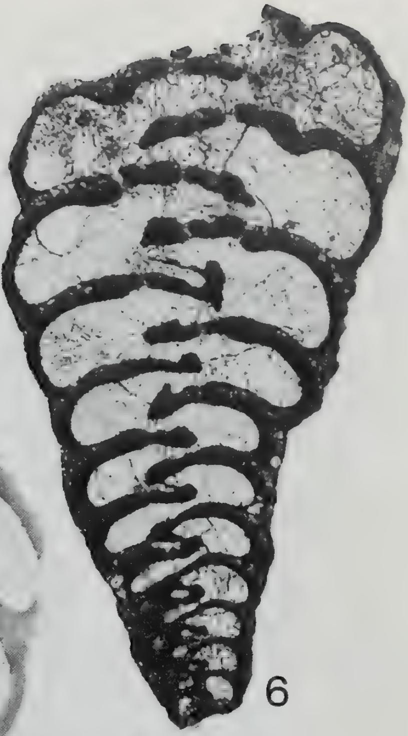

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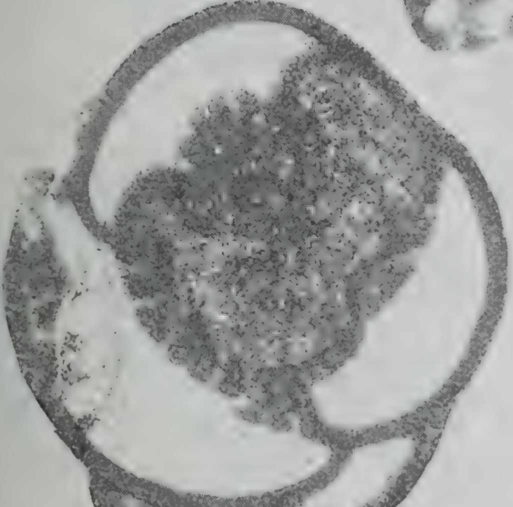

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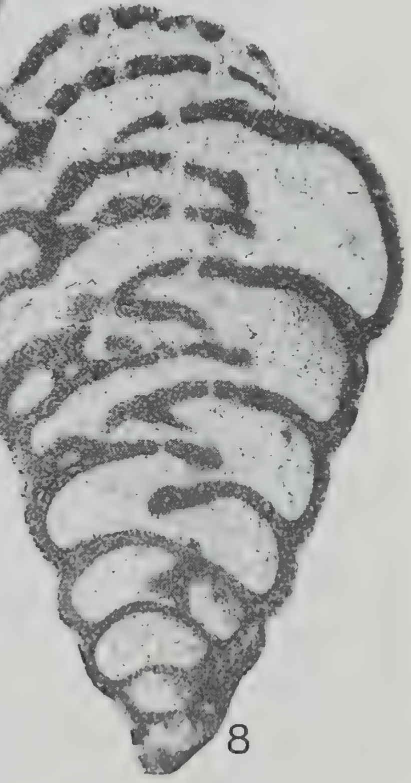

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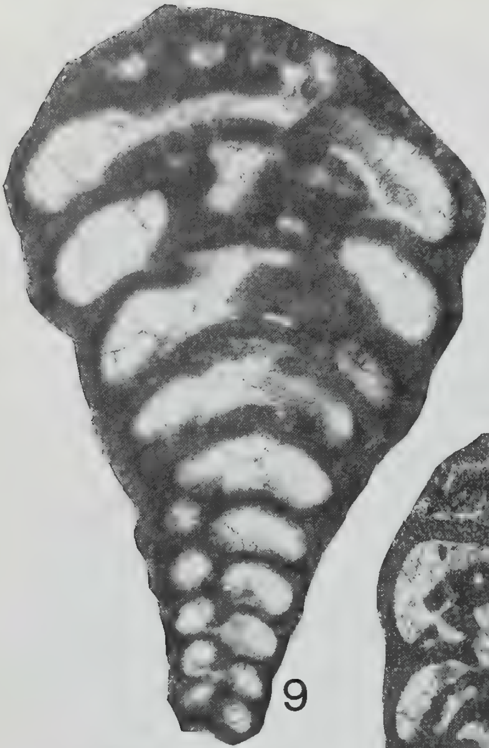
gs 4–8 *Praechrysalidina infracretacea* Luperto Sinni. Fig. 4, BMNH P 52582, from United Arab Emirates, well Umm Shaif-2, Upper Shuaiba Formation, Aptian; axial section (length 1000 μm), × 110. Fig. 5, BMNH P 52583, from Qatar, well Dukhan-23, 3710–3720 ft depth, Aptian; axial section (length 1010 μm), × 80. Fig. 6, BMNH P 52584, from United Arab Emirates, well Umm Shaif-2, Upper Shuaiba Formation, Aptian; axial section (length 2320 μm), × 45. Fig. 7, BMNH P 52585, from northern Iraq, Mosul region, well Mushorah-1, 7005–7010 ft depth, Qamchuqa Formation, Albian; equatorial section (breadth 1960 μm), × 45. Fig. 8, BMNH P 52586, from Oman, sample IT 86 908, Aptian; axial section (length 1760 μm), × 65.



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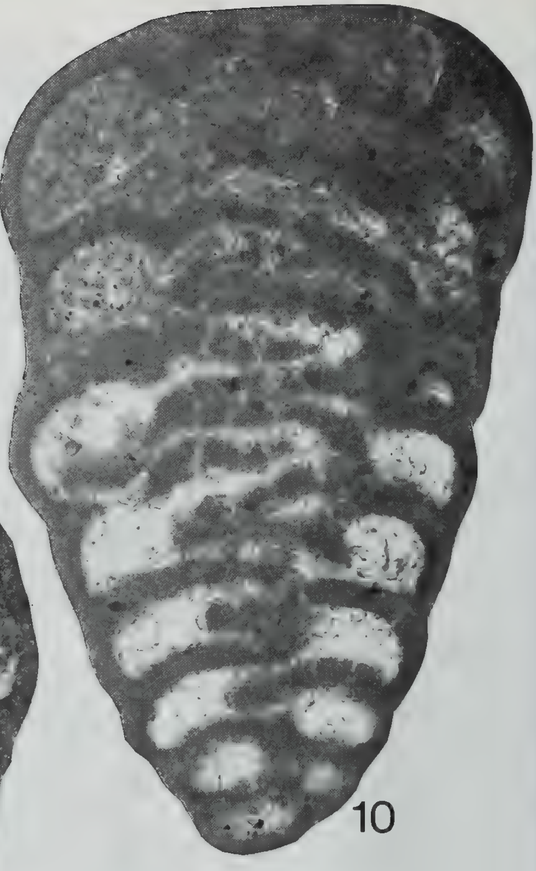

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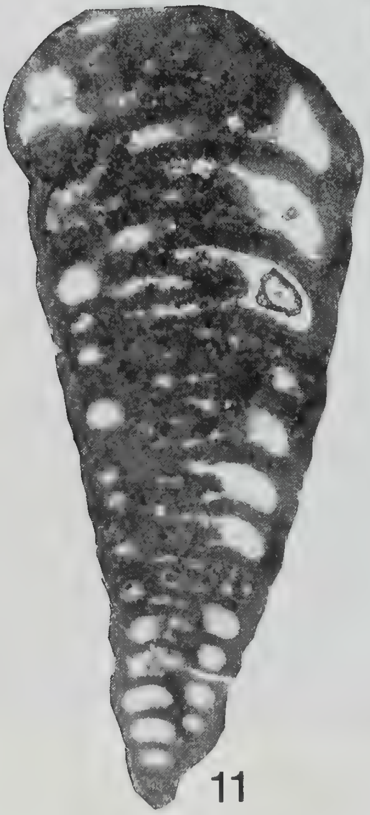

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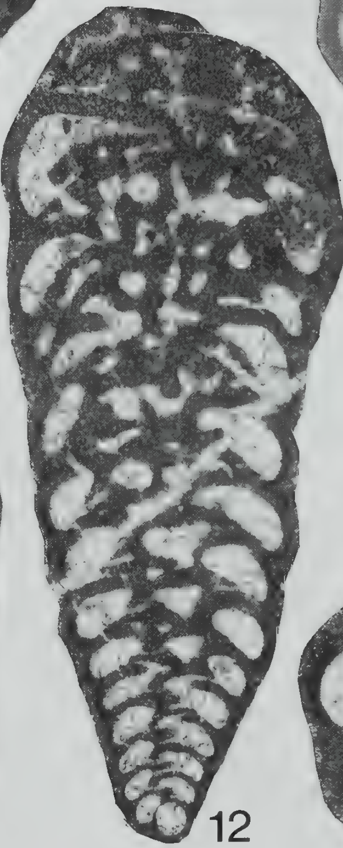

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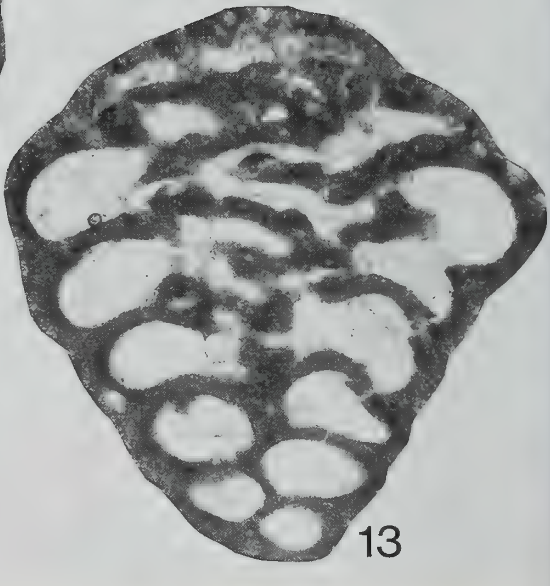

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The walls of the chambers often became protocanaliculate and then sometimes (but not always) canaliculate in the latest growth stages; this was illustrated by Luperto Sinni (*in* Schroeder & Neumann, 1985: pl. 6, fig. 10) for one topotype P. *infracretacea*, but other specimens (e.g., Figs 4–6) have walls which remain solid.

Praechrysalidina infracretacea Luperto Sinni was known to Henson and his associates, in the Iraq Petroleum Company, as '*Pseudochrysalidina* MC/2' ('MC' probably being a record of its first recognition by Max Chatton). It occurs in the Hauterivian of well Dukhan-2, Qatar (Figs 2a–c) and was recognized by them to occur in the Aptian of Dukhan well 23, Qatar (Fig. 5), and in the Albian–Barremian Qamchuqa Limestone Formation of northern Iraq (e.g. in well Mushorah-1, at 7005–7010 ft to 7560–7565 ft depth) (Fig. 7). We have also recognized it in the Aptian drilled off-shore in the United Arab Emirates (Figs 3, 4, 6) and outcropping in Oman (Fig. 8).

The evolution from *Praechrysalidina* into *Dukhania* was gradational and continuous (Figs 13, 14, 15). The umbilicus and the covering flaps broadened, and structurally supportive pillars developed between successive flaps. The pillars appear o have arisen from the outer, distal surfaces of later flaps, extending to approach, and then reach, the ventral surfaces of ucceeding flaps (Fig. 14). This is opposite to the way in which he inter-flap pillars seem to arise in *Paravalvulina* (p. 140). Also, the evolution into *Dukhania* was marked by a broadening of the test, which tapered more rapidly (Figs 13–15), and he developments of terminal biseriality. This was independent of, and distinct from, the evolution of *Praechrysalidina* nto *Chrysalidina* (Figs 9–12), when the slender, slowly tapering test and terminal triseriality were retained, even though nterflap pillars were also developed.

Genus ***DUKHANIA*** Henson, 1948

TYPE SPECIES. *Dukhania conica* Henson, 1948.

DIAGNOSIS EMENDED. A chrysalidinid with (megalospheric) riserial coiling reducing to adult biseriality; in each chamber of each adult whorl, the primary, interiomarginal aperture is covered by a broad flap which is penetrated by multiple, areal, accessory pore-like apertures; internal pillars develop between successive apertural flaps; wall solid, sometimes becoming protocanaliculate, sometimes (but not always) becoming canaliculate in the last-formed chambers.

Dukhania conica Henson, 1948 Figs 17–26

1948 *Dukhania conica* Henson: 615; pl. 15, figs 2, 4, 5, 8; pl. 17, figs 2, 3.

DESCRIPTION EMENDED. Test calcareous, microgranular; nepinic and neanic chamber-walls may be imperforate and non-canaliculate, but, in some specimens, ephebic and even neanic chambers may have walls which become protocanaliculate and even canaliculate. The innermost and outermost surfaces of both walls and septa consist of relatively much smaller microgranules, and appear darker when seen in thin section; the innermost layer, at least, can be perforated by canaliculi when they are developed. The test-form is conical. The megalospheric test is initially triserial (the microspheric test being initially quinqueserial), becoming biserial in a late ontogenetic stage. The nepionic–ephebic primary aperture is simple, umbilical and interiomarginal, rapidly acquiring the additional, neanic–ephebic, multiple, cribrate, areal, accessory pore-like apertures which are situated in the increasingly convex and broad apertural flaps (the 'trematophore-like', 'central shield' of Henson, 1948); both apertural flaps of the last-formed chambers join medially, with a closed suture, and have a convexity distinct from that of the terminal faces of the last chambers which remain exposed marginally. Internally, pillars develop between the apertural flaps, producing a labyrinthic area central to the long axis of the test; the volumes of the chambers themselves, marginal to the flaps, lack pillars.

REMARKS. Henson (1949) stated that *Dukhania* should be considered a synonym of *Pseudochrysalidina* Cole; for this reason, many of the specimens of *D. conica* in the Henson and associates collection were re-labelled, by them, to read '*Pseudochrysalidina conica*'. We accept Henson's earlier view, and consider *Dukhania* to be phylogenetically and morphologically distinct.

DIFFERENTIATION. *Dukhania* differs from *Paravalvulina* in its triserial–biserial coiling mode. Also, the apertural flaps ('shields') of *Dukhania*, even in the earliest whorls, have a strongly convex curvature very similar to that of the true, intercameral septa (and, of course, the terminal faces of the last chambers); in *Paravalvulina* spp. (from Middle Jurassic to ?Hauterivian) the 'shields' are flattened or only slightly convex. *Dukhania* differs from *Chrysalidina* in its terminal biseriality, developed even though its test is much less elongate; both genera may develop canaliculi in some ontogenetically late chamber walls, but retain solid walls throughout much of their tests.

AFFINITY. The initial triseriality of the test, with possession in the earliest whorls of very convex, cribrate apertural 'shields' (apertural-umbilical flaps), shows the affinity of *Dukhania* to its ancestral *Praechrysalidina*. Specimens which possess all the characters of *P. infracretacea* in their early whorls begin to develop a few, heavy pillars between successive apertural flaps of the last-formed chambers (Figs 13, 17) and are morphologically intermediate between *P. infracretacea* and the descendant *D. conica* (see p. 115). The development of canaliculation only occurs in the walls of the largest specimens of *D. conica*, but it may be observed more clearly and

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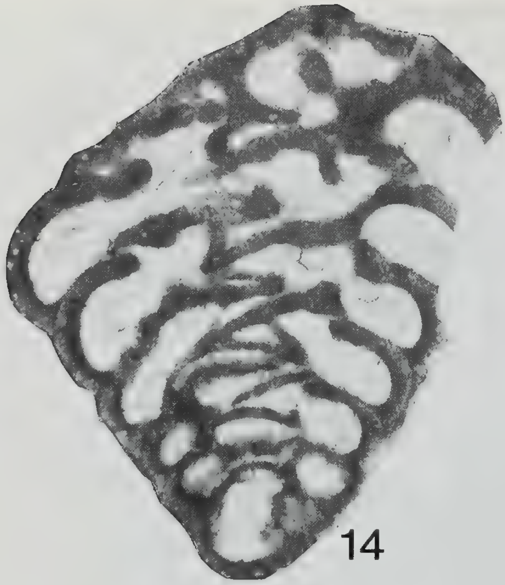
Figs 9–12 Morphologically intermediate forms between *Praechrysalidina infracretacea* Luperto Sinni and *Chrysalidina gradata* d'Orbigny. Fig. 9, BMNH P 52587, from northern Iraq, Mosul region, well Mushorah-1, 7560–7565 ft depth, Qamchuqa Formation, Albian; axial section (length 640 μm), with a few pillars developed in last two whorls only, × 155. Fig. 10, BMNH P 52588, from Jebel Madar, Oman, sample MS 91, Shuaiba Formation, early Aptian; axial section (length 2010 μm), with pillars only in the last-formed whorl, × 60. Fig. 11, BMNH P 52589, from United Arab Emirates, well Zakum-1, Shuaiba Formation, Aptian; axial section (length 2720 μm), with intermittently developed partial pillars in last whorls, × 40. Fig. 12, BMNH P 52590, Oman, sample WM 99 (I-240a), Wadi Mi'aidin, Natih Formation, Middle Cenomanian; axial section (length 3280 μm); same specimen as that figured by Simmons & Hart (1987: fig. 10.9.i), with the early half of the test being like *P. infracretacea* and the latter half being like *Chrysalidina*, with abundant pillars, × 35.

Fig. 13 Morphologically intermediate form between *Praechrysalidina infracretacea* Luperto Sinni and *Dukhania conica* Henson; BMNH P 52591, from northern Iraq, Mosul region, well Mushorah-1, 7435–7440 ft depth, Qamchuqa Formation, Albian; axial section (length 520 μm), with a few, incomplete pillars, in the last whorl only, × 145.



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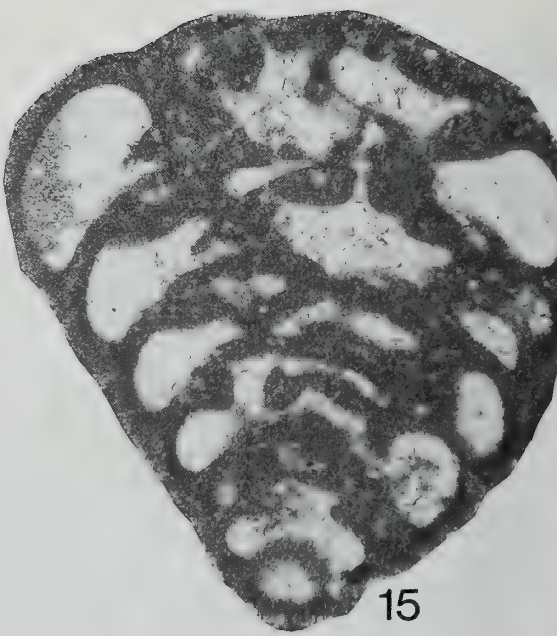

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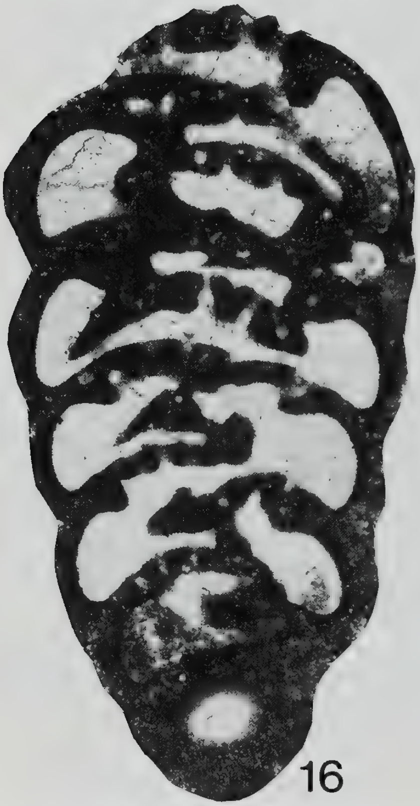

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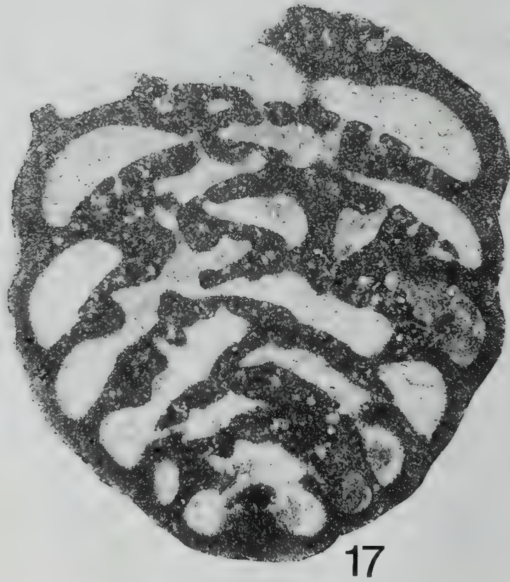

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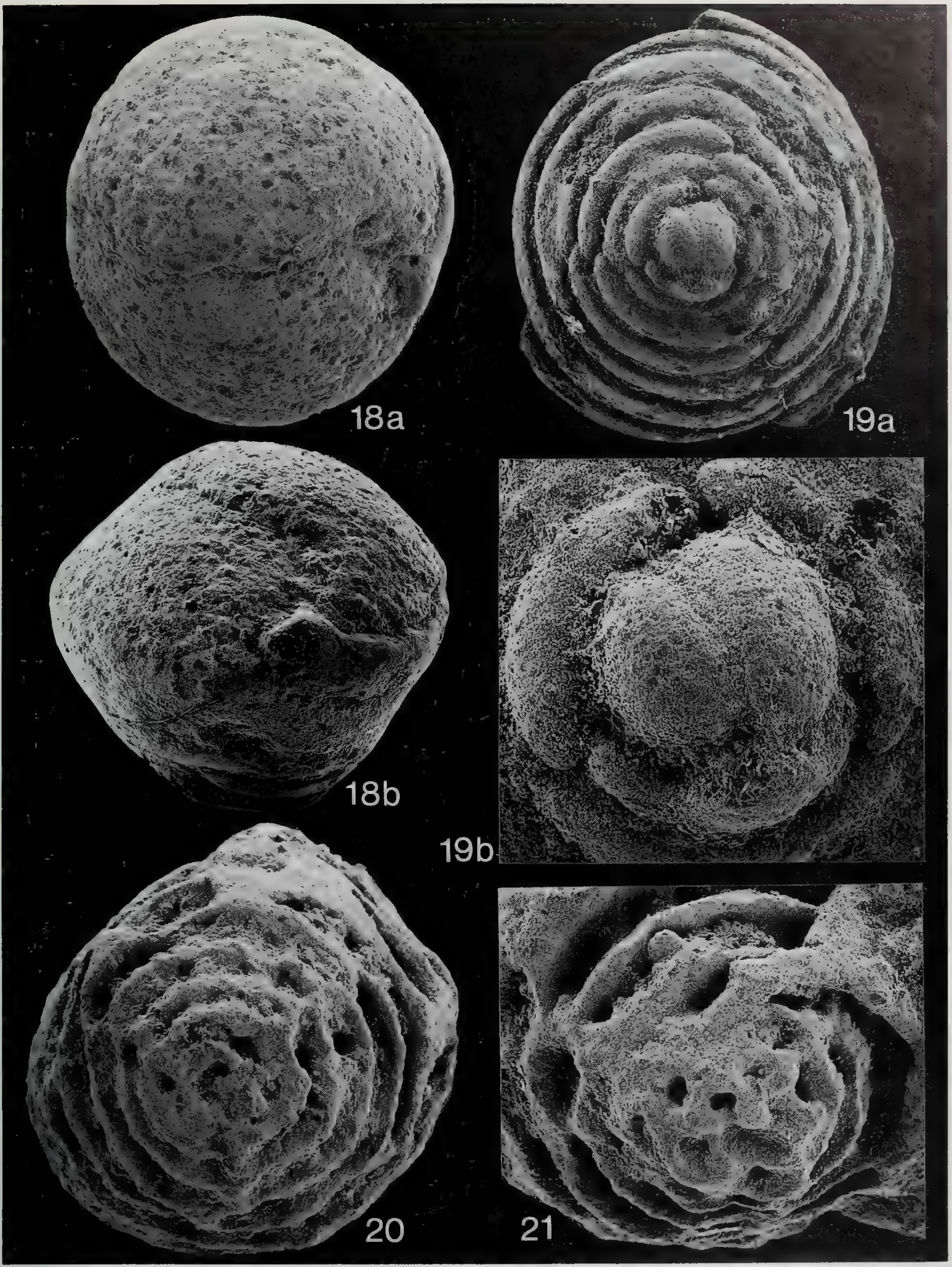
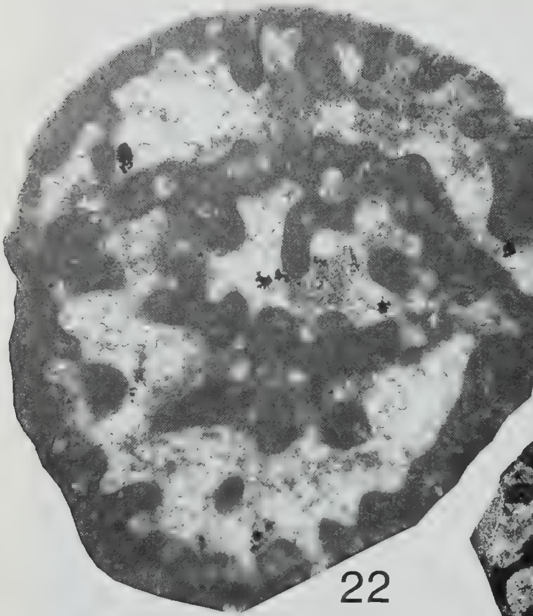
Figs 14–15 Specimens morphologically intermediate between *Praechrysalidina infracretacea* Luperto Sinni and *Dukhania conica* Henson. Fig. 14, BMNH P 52592, from northern Iraq, Mosul region, well Mushorah-1, 7470–7475 ft depth, Qamchuqa Formation, Albian; axial section (length 630 μm), with incomplete, and rare complete, pillars in last two whorls only; × 125. Fig. 15, BMNH P 52593, from Deh Luran, Iran, Cenomanian; axial section, with pillars developed throughout the umbilical areas of the last three whorls (and incomplete pillars in a previous whorl); this is a true *Dukhania*, but the chambers still retain the ancestral form (and the specimen was labelled 'Aff. *Dukhania conica* Henson' by Henson and his associates); axial section (length 1500 μm), × 55.

Fig. 16 Specimen morphologically intermediate between *Praechrysalidina infracretacea* Luperto Sinni and *Chrysalidina gradata* d'Orbigny: BMNH P 52594, from Tong-i-Mawari, Qashqai-Sarhad, Iran, 'Middle Cretaceous'; axial section (length 2620 μm), with a few pillars in the umbilical region of the last whorls, × 40.

Fig. 17 *Dukhania conica* Henson, paratype, BMNH P 52595, from 'Middle Cretaceous' (almost certainly Cenomanian), Kuh-i-Bingistan, Iran; axial section (length 960 μm), × 80.



igs 18–21 *Dukhania conica* Henson. Figs 18a–b, BMNH P 52596, from Qatar, well Dukhan-3, 2560–2565 ft depth, Cenomanian ('Middle Cretaceous'), originally determined by V. J. John but accepted by F. R. S. Henson, and believed by us to be virtually identical to the holotype of the species (BMNH P 39102); a, terminal view (showing terminal biseriality, and cribrate apertural pores calcite infilled), diameter 1880 µm, × 40; b, axial view, × 40. Figs 19a–b, paratype, BMNH P 52597, from Qatar, well Dukhan-3, 2030–2060 ft depth, Cenomanian; megalospheric form viewed from initial end, diameter 1620 µm; a, × 50; b, enlargement of nepiont, × 150. Figs 20–21, paratypes, from Qatar, well Dukhan-3, 2030–2060 ft depth, Cenomanian; microspheric forms, viewed from initial end. Fig. 20, BMNH P 52598, diameter of test 1640 µm, × 50. Fig. 21, BMNH P 52599, × 70.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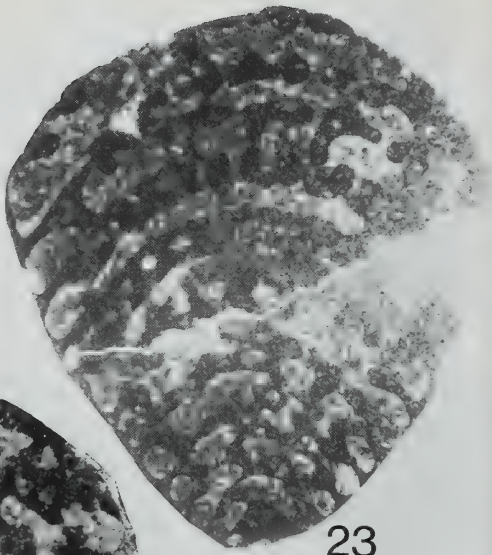
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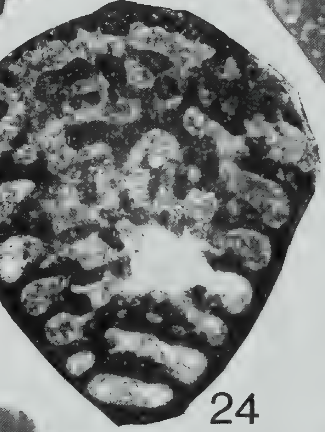
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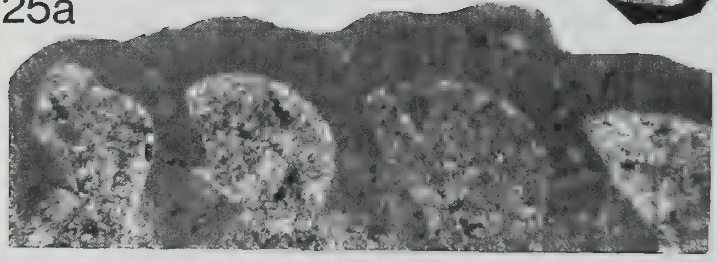

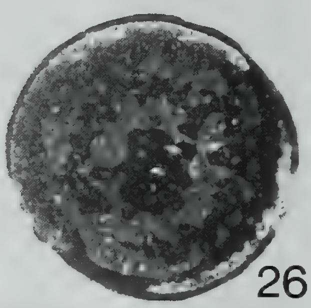
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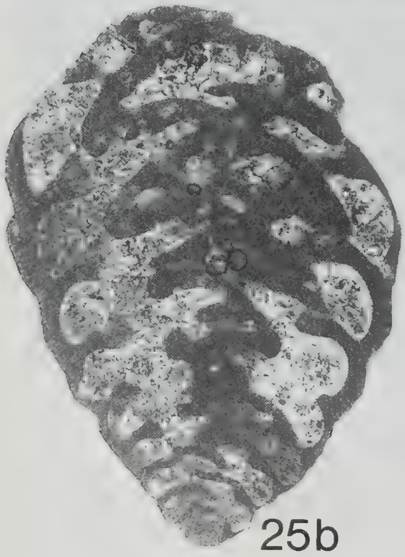
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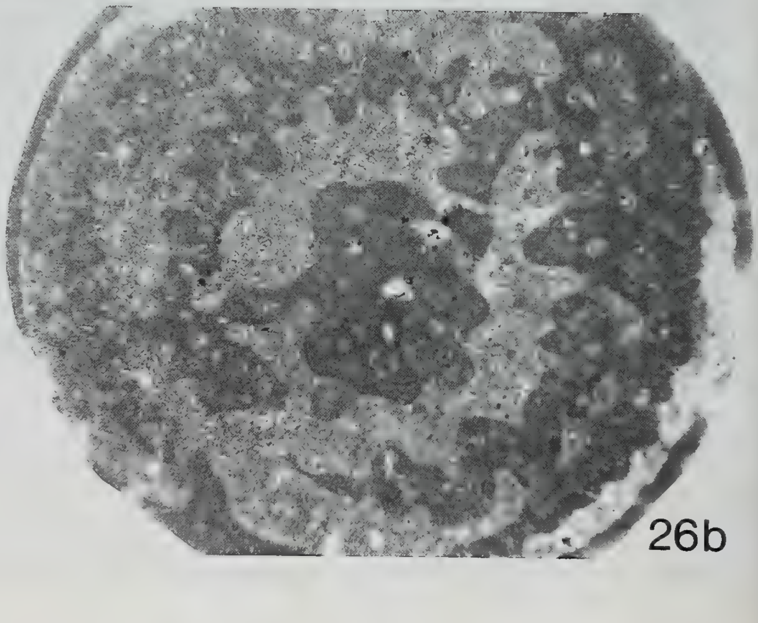
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frequently than in *Praechrysalidina*; that genus may only become protocanaliculate.

PROVENANCE OF TYPES. The holotype and paratypes of *Dukhania conica* Henson were obtained from well cuttings at 2540–2570 ft depth, well Dukhan-3, Qatar, from beds called 'Middle Cretaceous' by Henson (1948) but which also contained *Praealveolina cretacea* (d'Archiac) and which are therefore probably referable to the mid or late Cenomanian (see Schroeder & Neumann, 1985).

DISTRIBUTION. Of the other occurrences recorded by Henson (1948: 616), those from the Cenomanian limestone of the Bekhme Gorge, Iraq, have few or no pillars, are morphologically transitional from *Praechrysalidina*, and are closely similar to the specimen figured (as '*Chrysalidina* cf. *gradata* d'Orbigny') from Upper Cenomanian limestone of Lebanon by Hamaoui & Saint-Marc (1970: pl. 39, fig. 2).

Specimens which are clearly intermediate morphologically between *Praechrysalidina infracretacea* and *Dukhania conica* occur in the Albian Qamchuqa Formation of the Mosul region, Iraq, where incomplete pillars, which fail to span the distance between successive apertural flaps, occur (Fig. 13) and sometimes may be accompanied by a few, complete pillars developed only in the last one or two whorls (Fig. 14). The evolution from *Praechrysalidina* to *Dukhania* seems to have been gradual and continuous during the Albian and Cenomanian, with true *D. conica* first appearing in the Cenomanian (Fig. 106, p. 150).

Specimens (Fig. 15) from the Cenomanian of Deh Luran, Iran, which occur in micritic limestones with both *Praealveolina* and *Chrysalidina gradata*, which were listed by Henson (1948: 616) as ideotypes of *Dukhania conica*, but which were labelled 'Aff. *Dukhania conica*' by Henson and his associates, have inter-flap complete pillars developed in the last three whorls and are true *Dukhania*, but the shape and proportions of their chambers still recall their ancestry.

True *Dukhania conica* is known from Qatar (Figs 18–26), Iran (Fig. 17), Iraq (Dunnington *et al.* 1959: 230), and Oman (Smith *et al.* 1990: 37, fig. 6d). The last of these (from the Middle Cenomanian part of the Natih Formation of Oman) has even more numerous pillars than the typical *Dukhania conica*, but it lacks the heavy, thick pillars, thicker chamber walls, higher chambers and larger, more elongate test characteristic of *Chrysalidina gradata* (Figs 27–30 herein and, e.g., de Castro, 1981: pls 5, 6). With such random thin sections, it is often not possible to determine directly whether the test is terminally biserial (*Dukhania*) or triserial (*Chrysalidina*).

Dukhania conica is not yet known with certainty beyond the Middle East, and, consequently, it is believed to have been palaeobiogeographically more limited than either its ancestral *Praechrysalidina* or its contemporary *Chrysalidina*. It is probable that the evolution of *Dukhania* occurred in central Tethys and that (unlike *Chrysalidina*) it did not spread, eastwards or westwards, from this area.

STRATIGRAPHY. The evolution of *Dukhania* from *Praechrysalidina* (Fig. 106) may have begun in the Late Aptian; the descendant forms, in the Albian (e.g., Figs 13–16), with partly formed inter-flap pillars and low main chambers, probably should be distinguished from the pillarless ancestor by being named *Dukhania* sp. The genus may therefore be considered to range upwards from the Albian (or even late Aptian), but *D. conica* itself is not known in beds older than Cenomanian, and it is not known to have existed later than that stage. The record by Henson (1948: 616) of *D. conica* in 'Turonian limestones', at 'Rekhme, Palestine', has not yet been substantiated.

Genus ***CHRYSALIDINA*** d'Orbigny, 1839

TYPE SPECIES. *Chrysalidina gradata* d'Orbigny, 1839.

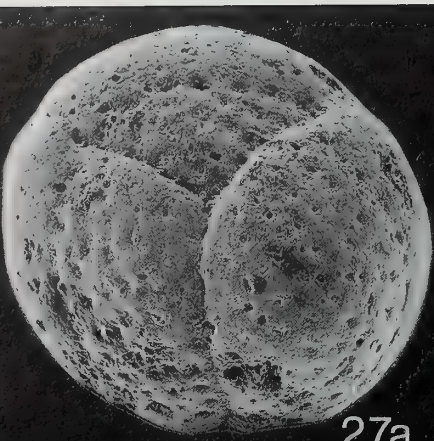
Chrysalidina gradata d'Orbigny, 1839 Figs 27–34

1839 *Chrysalidina gradata* d'Orbigny: 109.
1846 *Chrysalidina gradata* d'Orbigny: 194–195; pl. 21, figs 32, 33.

REMARKS. *Chrysalidina gradata* was first described by d'Orbigny (1839, 1846) from the Cenomanian of Île Madame (Charente-Maritime, off the west coast of France) and solid specimens of topotypes, and their orientated thin sections, have been well described and photomicrographed by Azzaroli & Reichel (1965), Neumann (1967: pl. 44), de Castro (1981, and in Schroeder & Neumann, 1985) and Loeblich & Tappan (1988: pl. 204). Other specimens, in thin section, have been photomicrographed from the mid to late Cenomanian of Aquitaine, south France (Neumann 1967, *loc.cit.*), Italy (Azzaroli & Reichel 1965, de Castro 1981: pl. 7), Greece (Septfontaine 1981), Oman (Simmons & Hart 1987: pl. 10.1; Smith *et al.* 1990), Yemen (Sartorio & Venturini 1988: 116), etc. The genus is monotypic, and probably is confined to the mid Cenomanian and the earlier part of the late Cenomanian; Turonian records (Loeblich & Tappan 1988: 186) have yet to be confirmed.

As noted above, the species evolved smoothly from *Praechrysalidina infracretacea* (Fig. 106) by developing higher chambers, heavy inter-flap pillars in the umbilicus, and a longer (and larger) adult test which nevertheless retained triseriality to the end of its life. The evolution seems to have been slow and completely gradational; although it began in the late Aptian (Figs 10–11) and continued through the Albian (Fig. 9), with the beginnings of the development of pillars in slender, triserial tests (which were, otherwise, typical *Praechrysalidina*), true *Chrysalidina* did not appear until the Cenomanian. Even then, specimens occur which lack pillars in the neanic umbilicus, at a stage of growth when the test could remain as slender as that of the ancestral (and by now extinct) *P. infracretacea* (Fig. 12). The typical

Figs 22–26 *Dukhania conica* Henson, from Qatar, well Dukhan-3, Cenomanian. Fig. 22, paratype, BMNH P 39105, from 2550–2560 ft depth; equatorial section (diameter 1500 μm), × 60. Fig. 23, topotype, BMNH P 52600, from 2560–2565 ft depth; axial section (length 2160 μm), × 35. Fig. 24, paratype, BMNH P 39104, from 2540–2570 ft depth; axial section (length 2080 μm), × 30. Figs 25a–b, paratype, BMNH P 52601, from 2540–2570 ft depth; a, wall with canaliculi, × 890; b, whole axial section (length 2060 μm), × 35. Figs 26a–b, paratype, BMNH P 52602, from 2030–2060 ft depth; a, equatorial section (breadth 1840 μm), showing ultimate biseriality, × 20; b, enlargement, showing umbilical pillars, × 515.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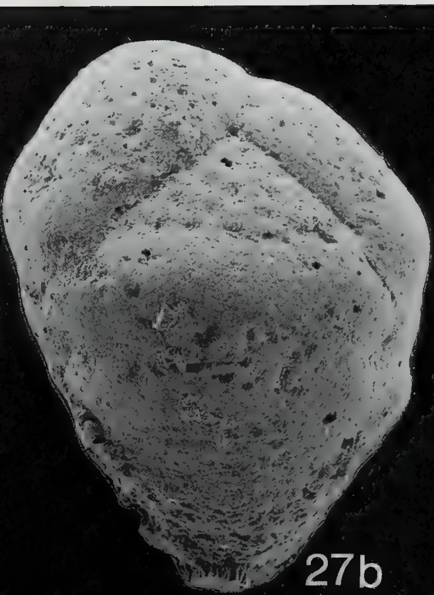
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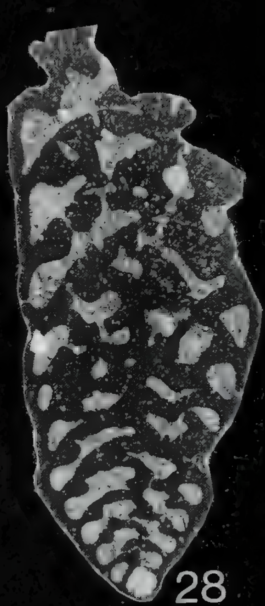
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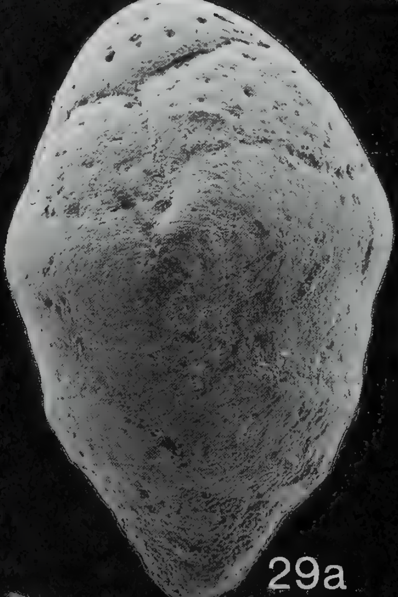
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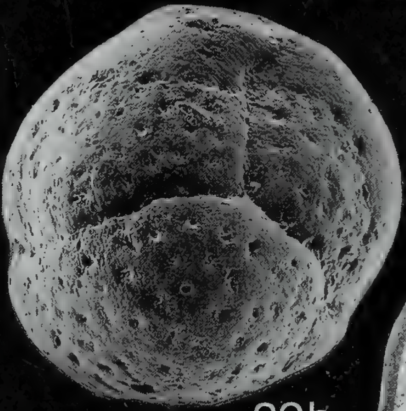
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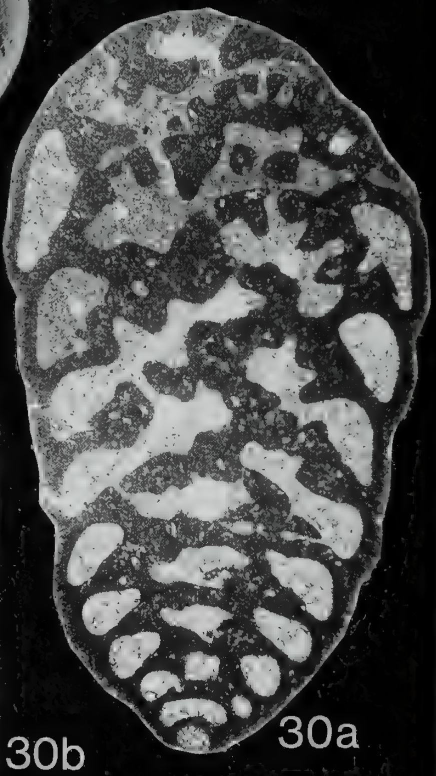
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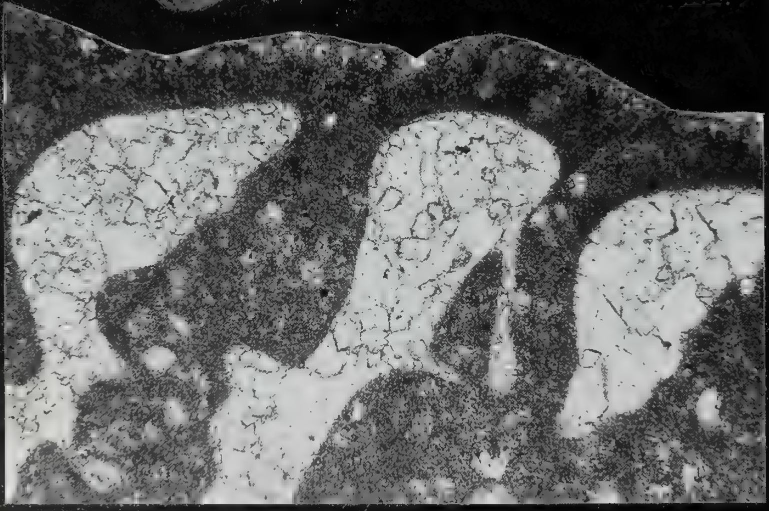
30b

C. *gradata* (Figs 27–30) rapidly tapered initially, in its neanic growth stage, although its ephebic chambers enlarged much more slowly; heavy umbilical pillars characteristically developed in all post-nepionic whorls.

The walls of many specimens of *Chrysalidina gradata* emain solid throughout growth (e.g., the topotypes illust-ated here, Figs 27–29, and those photomicrographed by de Castro, 1981: pls 5, 6); this is not an appearance resulting rom diagenetic alteration, because the presence and orienta-ion of intramural quartz grains would have prevented the primary development of protocanaliculation and canaliculi. However, other topotypes show the development of protocanaliculation or canaliculi even in the ontogenetically early walls (Figs 30a–b herein, and, e.g., Loeblich & Tappan, 1988: pl. 204, fig. 5). The canaliculi of some late Cenomanian, talian specimens are so clear that de Castro (1981: pl. 7) called them '*Chrysalidina* cf. *gradata*'. However, we can see no way to separate taxonomically the solid walled forms, the protocanaliculate forms and those with canaliculi; they are otherwise structurally identical, are indistinguishable without hin-sectioning or the SEM examination of partly-eroded pecimens, occur in the same assemblages and appear to ave the same stratigraphic range within the mid to late Cenomanian.

Accordiella conica Farinacci is a monotypic genus which was first recorded from the Lower Senonian of Italy (Farinacci 962), when it was noted that it was also known from he Coniacian–Santonian of France (Aquitaine) and Spain. It as not yet been observed in the Middle East or recorded rom the Turonian (for example, it was not recorded from he Albian–Turonian interval of the Mediterranean region y Schroeder & Neumann, 1985). Nevertheless, the evolu-on of *Accordiella* from *Chrysalidina* (as postulated by eptfontaine, 1981: 184 – Farinacci, 1962: 10, suggested an volution directly from *Dukhania*) is very likely to be correct: ll that is required morphologically is to widen the umbilicus urther, fill it with more closely spaced, more abundant illars, and to increase the number of chambers, around he broader umbilicus, to four (i.e., to achieve quadriseri-lity, at least in the adult) (Farinacci 1962: pl. 1, figs 1–7). Morphologically intermediate forms may be expected in the uronian.

The lineage is unknown in the Campanian and younger rata and probably became extinct at this time. As noted bove, it is probable that the Chrysalidininae should exclude ther, Cenozoic taxa (such as *Vacuovalvulina* and *Pseudo-hrysalidina*), but this needs further study.

Subfamily **PARAVALVULININAE** nov.

IAGNOSIS. Test quadriserial or quinqueserial initially, ecoming quadriserial in neanic growth, and then quinque-rial or quadriserial or triserial in the adult.

KEY TO GENERA INCLUDED

1. Umbilicus or pseudoumbilicus concave, with apertural flaps or lips attached to the lower part of the exposed apertural faces of the chambers; no internal, umbilical pillars:
    1.1. Primary and accessory apertures interiomarginal; no accessory areal, cribrate apertures; apertural flaps of successive whorls are well separated:
        1.1.1. Test quadriserial in adult: septa flattened or very weakly convex; narrow, hollow umbilicus: *Redmondoides* gen. nov. (Bajocian–Oxfordian–?Kimmeridgian).
        1.1.2. Test initially quadriserial, becoming triserial in adult; no true umbilicus:
            1.1.2.1. Septa and terminal faces flat or concave: *Riyadhoides* gen. nov. (late Bajocian–Tithonian).
            1.1.2.2. Septa and terminal faces highly convex: *Riyadhella* Redmond, 1965 (Bajocian–Kimmeridgian).
    1.2. With accessory, areal, cribrate apertures; umbilical-apertural flaps of successive whorls are broad and are axially separated by only narrow spaces (they may be appressed axially); adult test quadriserial or quinqueserial: *Pseudomarssonella* Redmond, 1965 (Bathonian–Callovian).
2. Umbilicus covered by convex umbilical flaps which are attached to the top of the apertural faes of the chambers; with accessory, areal, cribrate apertures; internal pillars between successive umbilical flaps; early test quadriserial, adult becoming triserial: *Paravalvulina* Septfontaine, 1988 (Bathonian–Valanginian–?Hauterivian).

Genus ***REDMONDOIDES*** nov.

TYPE SPECIES. *Pseudomarssonella media* Redmond, 1965.

DIAGNOSIS. A chrysalidinid with a test which is quinqueserial or quadriserial initially, becoming quadriserial in the adult; adult primary aperture interiomarginal, umbilical, with an apertural flap or lip (which is not penetrated by areal accessory apertures) projecting from the lowest part of the apertural face above the aperture; no internal, umbilical pillars; terminal faces and septa are flattened or only weakly convex, and make distinct angles with the uninflated chamber walls.

NAME. In further recognition of C. D. Redmond's work on Arabian Mesozoic foraminifera; gender – masculine.

DIFFERENTIATION AND AFFINITY. *Redmondoides* differs from *Pseudomarssonella* Redmond in that the latter has broad umbilical flaps, penetrated by areal, cribrate, pore-like accessory apertures; these flaps span much or all of the umbilicus and fuse to the opposite chambers (or their flaps) of the same whorl, partly or wholly closing the accessory interiomarginal aperture. In *Redmondoides* the umbilical flaps (or 'lips') are much narrower and the interiomarginal aperture remains unimpeded. *Riyadhoides* has no umbilicus or umbilical flaps, and also differs in its quadriserial–triserial coiling (a coiling mode which can result in a distinctly parallel-sided adult test, but which can also produce a conical, rapidly tapering one).

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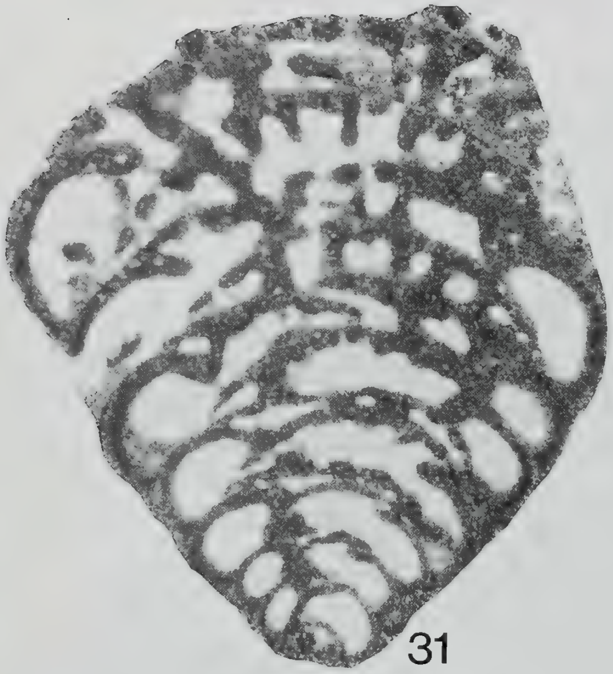
gs 27–30 *Chrysalidina gradata* d'Orbigny, topotypes, from Île Madame, Charente Inférieur, France, Cenomanian; Figs 27a–b, BMNH P 52603, terminal and axial views (length 1940 µm), × 40. Fig. 28, BMNH P 52604, axial section (length 3860 µm), × 20. Figs 29a–b, BMNH P 52605, axial and terminal views (length 2120 µm), × 40. Figs 30a–b, BMNH P 53606, axial section (length 3260 µm); a, × 30; b, detail showing solid septa with randomly arranged calcareous microgranules and included silt grains, and protocanaliculate–canaliculate chamber walls, × 105.



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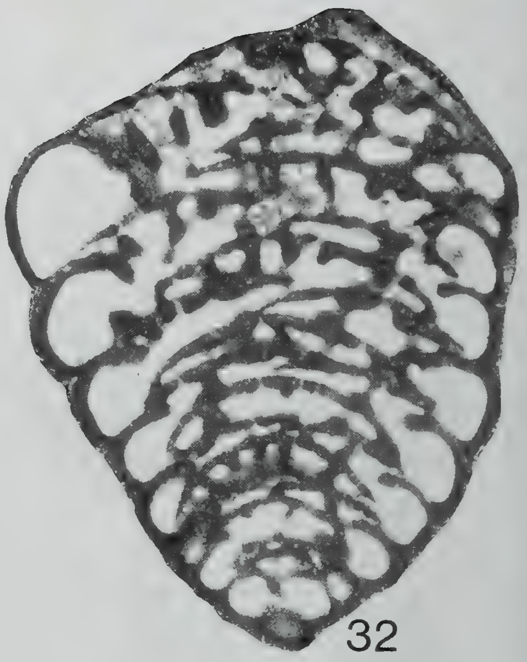

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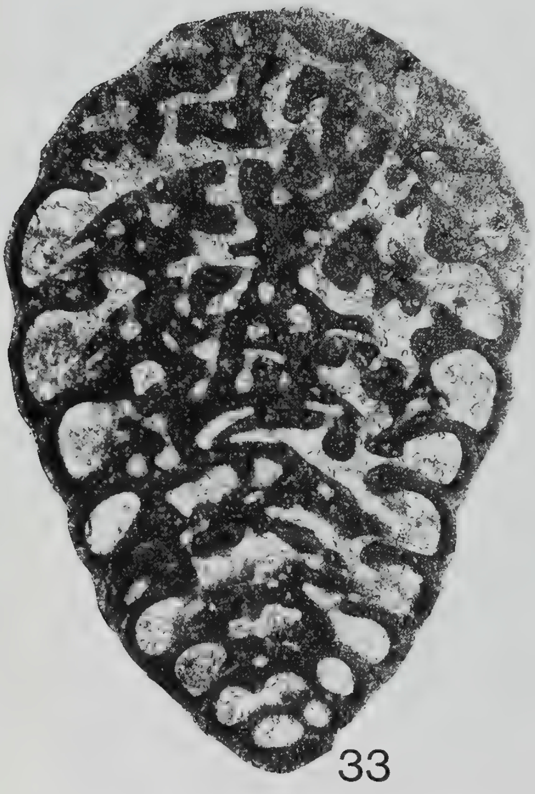

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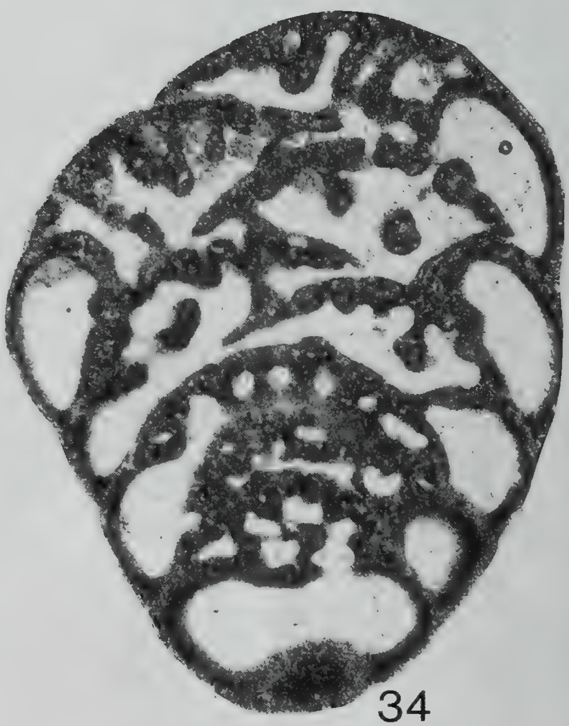

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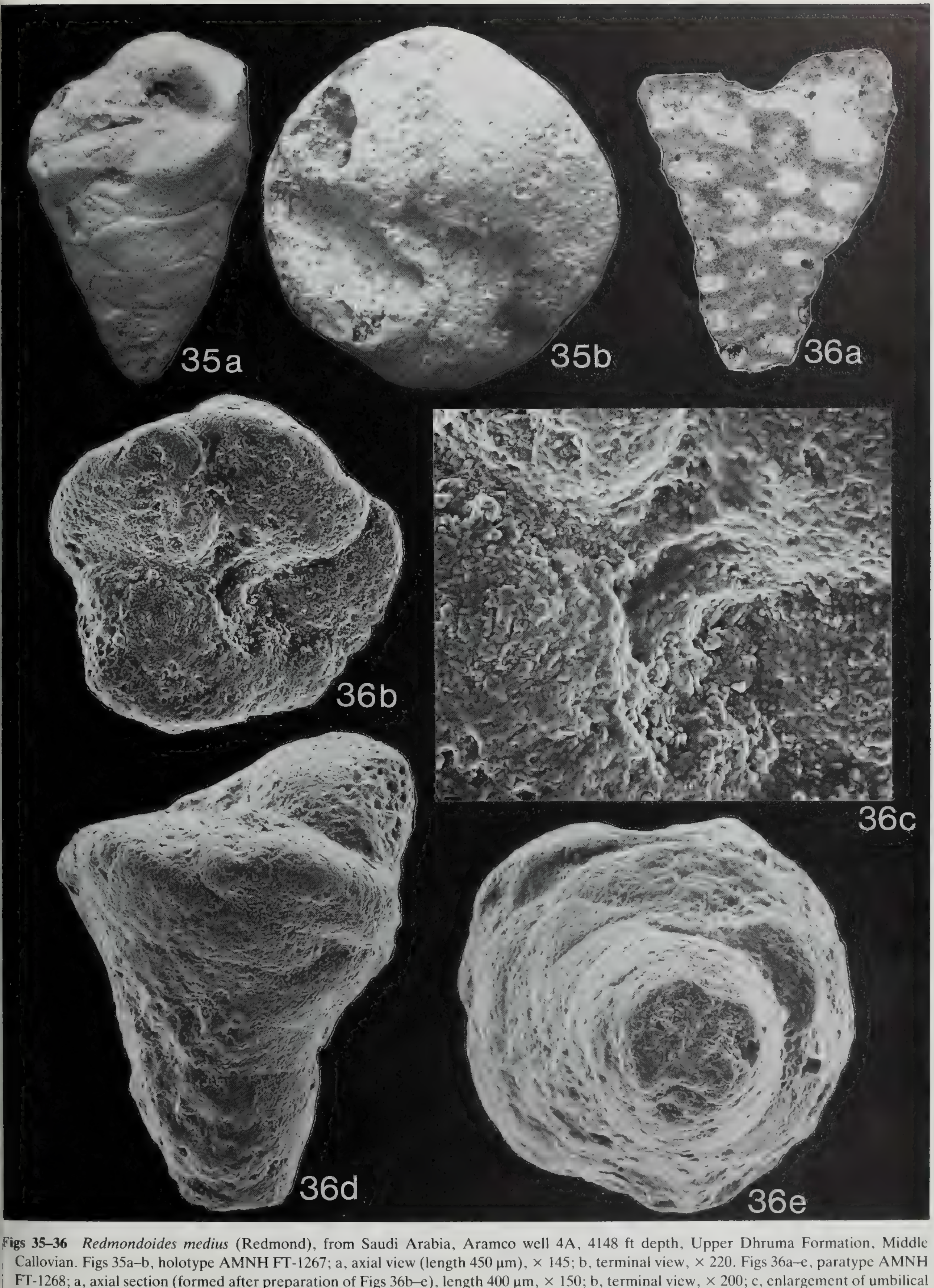
Figs 31–34 *Chrysalidina gradata* d'Orbigny. Axial sections. Figs 31–32, 34, from Oman, Jebel Madamar, Natih Formation, Cenomanian. Fig. 31, BMNH P 52607, sample WMA 1 (length 2020 μm), × 45. Fig. 32, BMNH P 52609, sample WMA 3, same specimen as that figured by Smith, Simmons & Racey, 1990, fig. 6d (length 2450 μ), × 35. Fig. 33, from Deh Luran, Iran, Cenomanian, BMNH P 39127, from the same limestone thin section as the specimen figured by Henson, 1948: pl. 15, fig. 8 (length 2700 μm), × 40. Fig. 34, BMNH P 52608, sample WMA 1 (length 2400 μm), × 40.



Figs 35–36 *Redmondoides medius* (Redmond), from Saudi Arabia, Aramco well 4A, 4148 ft depth, Upper Dhruma Formation, Middle Callovian. Figs 35a–b, holotype AMNH FT-1267; a, axial view (length 450 μm), × 145; b, terminal view, × 220. Figs 36a–e, paratype AMNH FT-1268; a, axial section (formed after preparation of Figs 36b–e), length 400 μm, × 150; b, terminal view, × 200; c, enlargement of umbilical area, × 500; d, axial view (showing open canaliculi in wall of last chamber), in same attitude as the thin section (Fig. 36a), × 220; e, initial view, showing initial quadriseriality, × 220.

Riyadhella differs in its highly convex terminal faces and septa, which do not form distinct angles with the lateral chamber walls; it also lacks an umbilicus and an apertural flap, and has terminal triseriality.

It is supposed that *Redmondoides* gave rise to *Pseudomarssonella* in the Bathonian, which, in turn, gave rise to *Paravalvulina* Septfontaine, also in the Bathonian.

SPECIES INCLUDED AND STRATIGRAPHY. In addition to the type species, the following are now included in *Redmondoides*: *Pseudomarssonella biangulata* Redmond (synonym of *R. medius*), *P. inflata* Redmond, *P. primitiva* Redmond, *Riyadhella rotundata* Redmond, *Valvulina lugeoni* Septfontaine. The known stratigraphic range of the genus is Bajocian–Oxfordian–?Kimmeridgian. It is known (principally by specimens referable to *Redmondoides lugeoni*) in marine deposits from western to eastern Tethys (from southern Europe to Borneo). Random thin sections of specimens, which may be species of *Redmondoides,* are known to us from very early Cretaceous (possibly Valanginian–Hauterivian), Tethyan limestones, but the seriality of their chamber arrangement is unknown and their generic identity cannot yet be established.

In the following descriptions, the species originally described by Redmond are described first, and these are followed by an emended description of *Redmondoides lugeoni* (Septfontaine).

Redmondoides medius (Redmond, 1965) Figs 35–37

1965 *Pseudomarssonella media* Redmond: 135; pl. 1, figs 11–13.
1965 *Pseudomarssonella biangulata* Redmond: 134; pl. 1, fig. 1.
1989 *Pseudomarssonella bipartita* Redmond; Delance & Ruget: 206; pl. 3, fig. 16 (*non* Redmond, 1965).

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present; the walls are initially solid, but may become canaliculate in the last-formed chambers. The test may be quinqueserial in the nepionic growth stage but is quadriserial in the neanic and ephebic stages. The test is subcircular in equatorial section. The neanic growth stage may taper slowly, at about 30°–40°, but ephebic growth enlarges the chambers more rapidly, so that the adult test is a cone tapering at about 50° (in some specimens, the 50° taper occurs in all growth stages).

The chambers are about three times as broad as high, and constitute the outer 40% or more of the test diameter; the central 15%–20% of the equatorial diameter is umbilical. The terminal face of each chamber is about as thick as the lateral wall, but the intercameral septa are virtually doubled in thickness by being composed of two layers – the terminal wall of the earlier chamber plus the basal wall of the succeeding chamber. The double-thickness septum is about one-third as high as the chambers (i.e., the lumina of a chamber is about twice as high as the septum which precedes it). The terminal faces and the septa are flattened, and make angles of 70°–90° with the lateral walls. The lateral walls are flattened or slightly concave. The intercameral sutures are very shallowly and narrowly depressed or are not depressed at all.

The apertural face is very low. The interiomarginal, umbilical aperture is furnished with a thin, narrow, apertural lip. The umbilicus is depressed and empty.

REMARKS. Redmond (1965) distinguished *Pseudomarssonella biangulata* from *P. media* by the supposed 'break between growth stages' in the former, whereas the latter had 'sides diverging at a uniform rate'. However, a paratype of *P. media* (Fig. 36) has the same slender neanic stage and more widely conic ephebic stage as the holotype of *P. biangulata* (Fig. 37).

The present authors can find no way of satisfactorily distinguishing between the two taxa, and, as first revisers (ICZN Article 24), choose *P. media* to be the senior synonym. Redmond (1965) stated that *P. biangulata* was 'common in the upper part of the middle Dhruma Formation', but only the holotype of this species (no paratypes or other specimens) was deposited; in comparison, the holotype and two paratypes (one now sectioned) of *P. media* ('abundant . . . [in] the upper Dhruma Formation') were deposited.

The specimen figured by Delance & Ruget (1989) as '*Pseudomarssonella bipartita*' is poorly preserved and its identity is uncertain; however, it appears to have terminal quadriseriality and a small, flattened umbilical area, which, together with its overall test shape, indicates that it should be referred to *Redmondoides medius*.

DIFFERENTIATION. *Redmondoides medius* is less slender and less slowly tapering than *R. primitivus*, and more slender and more slowly tapering than *R. inflatus*. Otherwise, these three 'species' are very similar. Redmond and his co-workers in Aramco succeeded in distinguishing them; further work is needed before one can be certain that the distinctions can be maintained.

Redmondoides rotundatus (Redmond) is distinguishable by its more broadly depressed intercameral sutures and more convex terminal faces. *R. lugeoni* (Septfontaine) also differs by its broader umbilicus and much broader apertural lip.

PROVENANCE OF TYPES. The type specimens of *R. medius* were obtained from Aramco stratigraphic well 4A (27°51′19″N, 44°54′47″E), from a core at 4148 ft depth, and that of *R. biangulatus* came from Aramco drill hole T 60 A (24°55′04″N, 45°59′08″E), from 80–90 ft depth.

STRATIGRAPHY. Redmond (1965) recorded '*Pseudomarssonella' biangulata* from the upper part of the middle Dhruma Formation ('Bathonian') and '*P.' media* from the upper part of the upper Dhruma Formation ('Callovian'); these intervals were referred by Powers (1968) to the *Dhrumaites* Zone limestone and shale ('Unit 8', uppermost Middle Dhruma) and the Hisyan (or Hishyan) Member (shales, 'Unit 10', upper Upper Dhruma), repectively. The former was regarded by Enay *et al.* (1987) as belonging to the Middle (or Late) Bathonian, and the latter as being referable to the Middle Callovian.

The specimens described by Delance & Ruget (1989) were obtained from the Bathonian of the Nivernais, France, east o the Loire, at about 47°10′N, 3°15′E.

Redmondoides inflatus (Redmond, 1965) Figs 38–3

1890 *Valvulina conica* Parker & Jones; Haeusler: 76; pl. 12 figs 27–35 (*non Valvulina triangularis* d'Orbigny var *conica* Parker & Jones, 1865)
1965 *Pseudomarssonella inflata* Redmond: 134–135; pl. 1 figs 4–5.

DIFFERENTIATION. This taxon seems to be identical to *R medius* (Redmond) except for the broader, more rapidl tapering test, in which the subconical test tapers at angles o

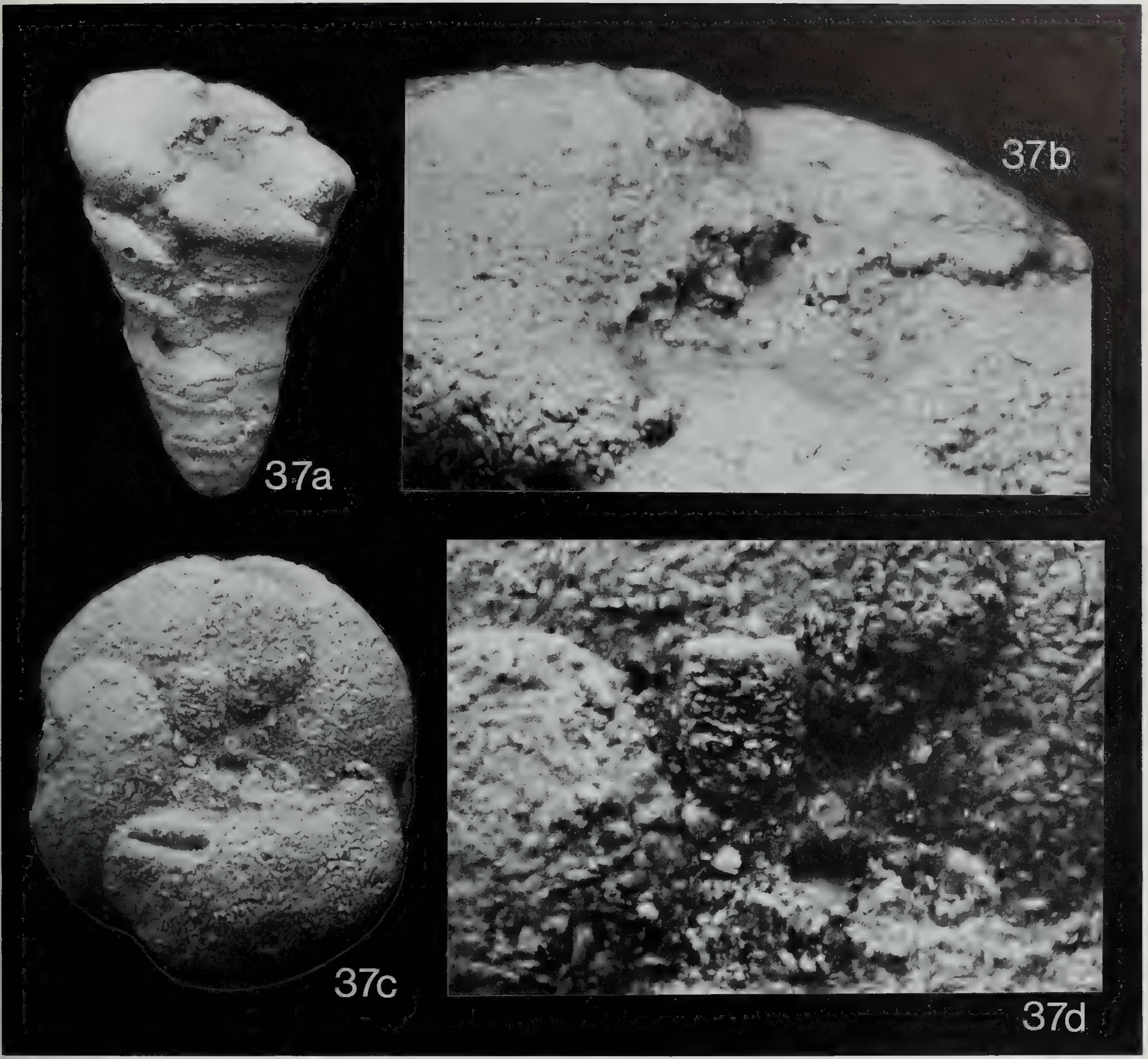


Fig. 37 *Redmondoides medius* (Redmond). Holotype of the synonymous *Pseudomarssonella biangulata* Redmond, AMNH FT-1264; from Saudi Arabia, Aramco T 60 A, 80–90 ft depth, Middle Dhruma Formation, mid or late Bathonian; a, axial view (length 380 μm), × 170; b, enlargement of apertural area, × 590; c, terminal view, × 270; d, enlargement of umbilical area, × 640, showing 'spicule-like' coating of the surface.

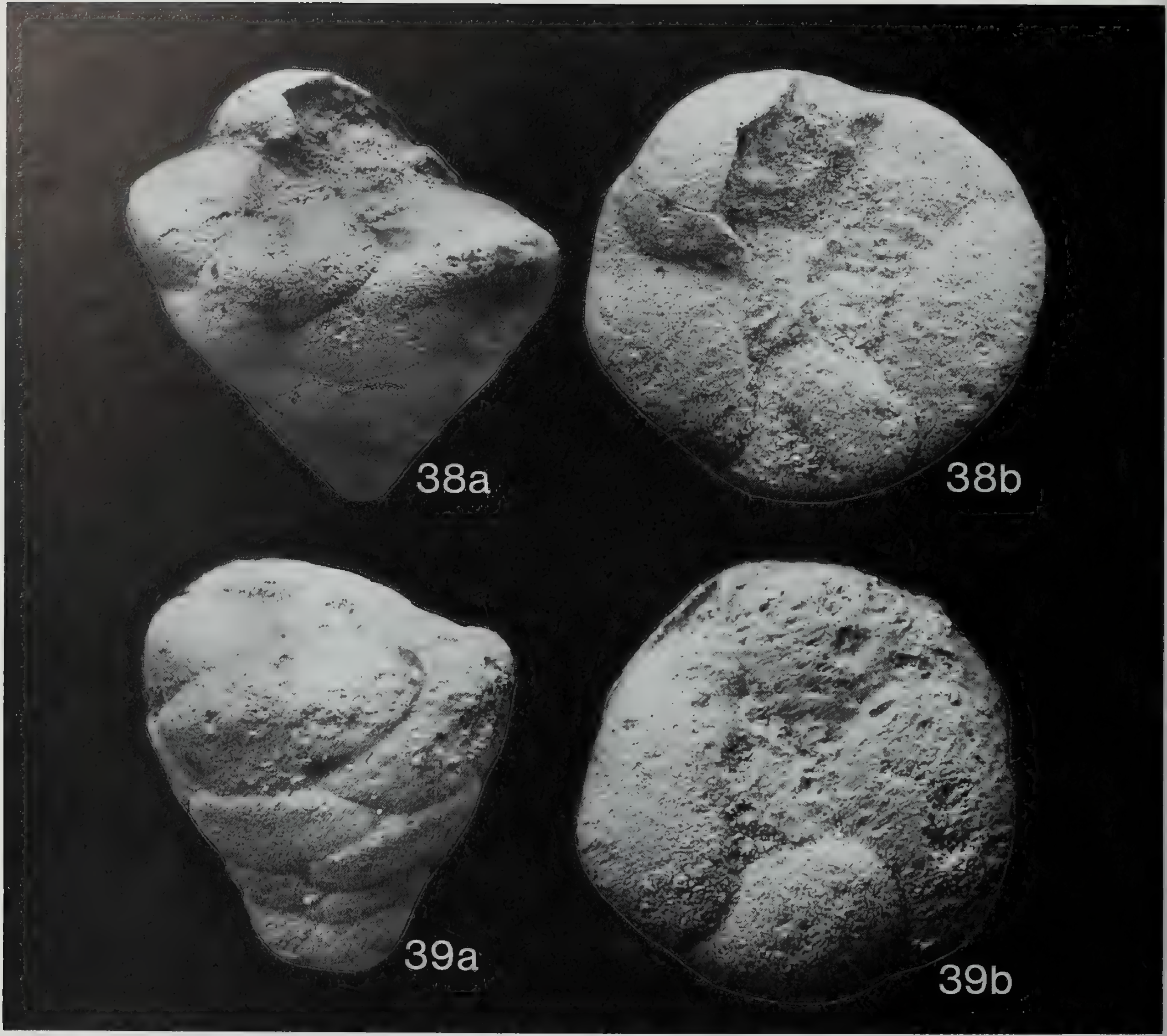
60° (paratype) to 80° (holotype), and the broader umbilicus (about 25% of the total test breadth).

REMARKS. Only the holotype and one paratype were deposited. There is insufficient information to confirm that this represents a species distinct from *R. medius*. However, the type specimens appear to be identical with those illustrated by Haeusler (1890) from the 'Transversariusschichten' (the '*Ammonites transversarius* Zone') of the Lower Oxfordian of Switzerland (Haeusler misidentified his specimens as the Cenozoic true *Valvulina*, *V. triangularis* d'Orbigny *conica* Parker & Jones, 1865); they have identical late quadriseriality, chamber and test shapes.

Redmond (1965) stated that there were 'five chambers in the final whorl'; the last chamber of the holotype is broken but could well have originally occupied about one-quarter of the final whorl, while the paratype is clearly quadriserial terminally.

PROVENANCE OF TYPES. From Aramco stratigraphic well 4A (as the type specimens of *R. medius*), core at 4524 ft depth.

STRATIGRAPHY. Recorded by Redmond (1965) from the 'upper part of the middle Dhruma Formation. Bathonian', the same as for the type of *R. biangulatus* (Redmond), the junior synonym of *R. medius* (Redmond). This interval would be that called 'Unit 8' by Powers (1968) or 'D6' by Enay *et al.*



Figs 38–39 *Redmondoides inflatus* (Redmond); from Saudi Arabia, Aramco well 4A, 4524 ft depth, upper Middle Dhruma Formation, mid or late Bathonian. Figs 38a–b, holotype, AMNH FT-1267; a, axial view (length 450 μm), × 145; b, terminal view, × 165. Figs 39a–b, paratype, AMNH FT-1268; a, axial view (length 420 μm), × 150; b, terminal view, × 165.

(1987); the latter considered it to be referable to the mid/late Bathonian.

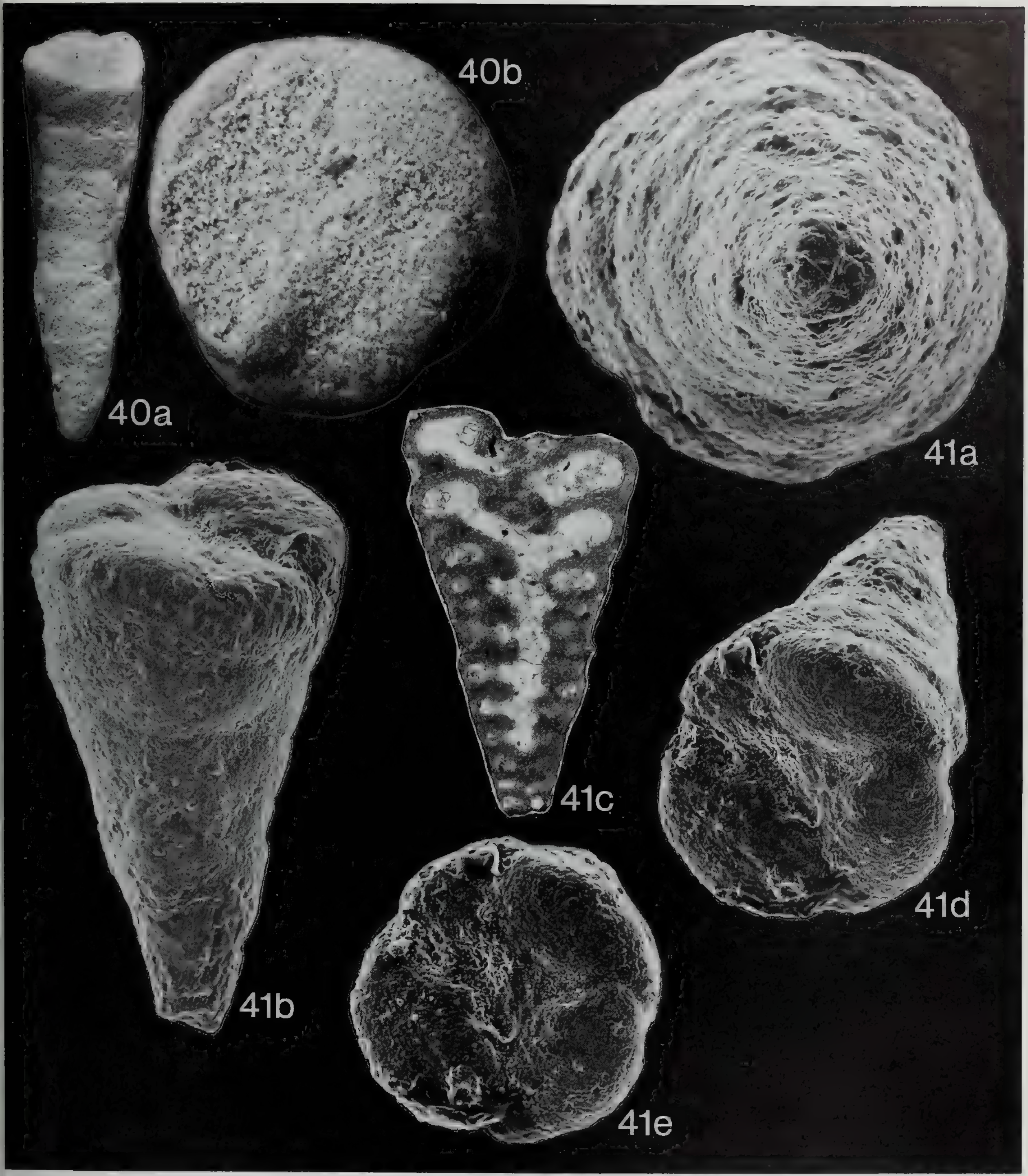
Redmondoides primitivus (Redmond, 1965) Figs 40–41

1965 *Pseudomarssonella primitiva* Redmond: 136; pl. 1, figs 16–18.

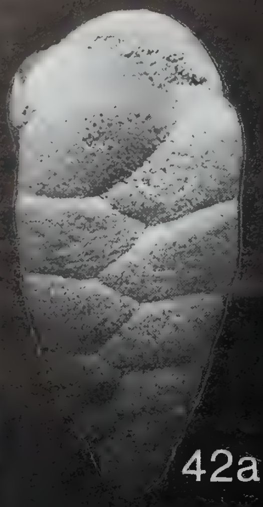
Description emended. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present. The walls are thin and solid, and no canaliculation is yet known. The test may be quinqueserial nepionically, but it is quadriseral throughout the remainder of growth. It is subcircular in equatorial section, and forms a narrow, slender cone, with a 30°–35° initial angle. The test may (as in the holotype) narrow after neanic growth, to taper terminally at only 20° or less, but it may retain a constant rate of chamber enlargement (and constant angle of taper) throughout ontogeny.

The chambers are about three times as broad as high and constitute the outer 35% of the test diameter; the central 30% of the equatorial diameter is umbilical. The terminal face of each chamber is about as thick as the lateral wall, and the intercameral septa are only partially thickened by the deposition, over their outer parts, of a thin basal layer of the succeeding chamber wall. Even the double-thickened septa may only be a quarter as high as the chambers theselves.

The terminal faces and the septa are flattened or only very weakly convex, and make angles of 90° or more with the uninflated or only slightly inflated lateral chamber



igs 40–41 *Redmondoides primitivus* (Redmond); from Saudi Arabia, Riyadh Water Well-1, 2400–2410 ft depth, Middle Dhruma Formation, late Bajocian. Figs 40a–b, holotype AMNH FT-1277; a, axial view (length 680 μm), × 100; b, terminal view, × 290. Figs 41a–e, paratype AMNH FT-1278 (Figs 41a, b, d, e are the original, solid specimen, now sectioned as Fig. 41c); a, initial view, × 250; b, axial view (length 540 μm), × 175; c, axial section, × 130; d, oblique terminal view, × 175; e, terminal view, × 175.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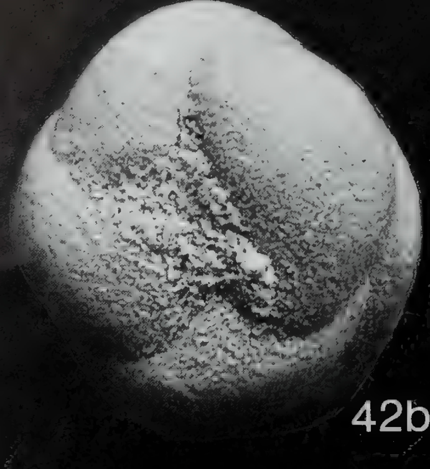
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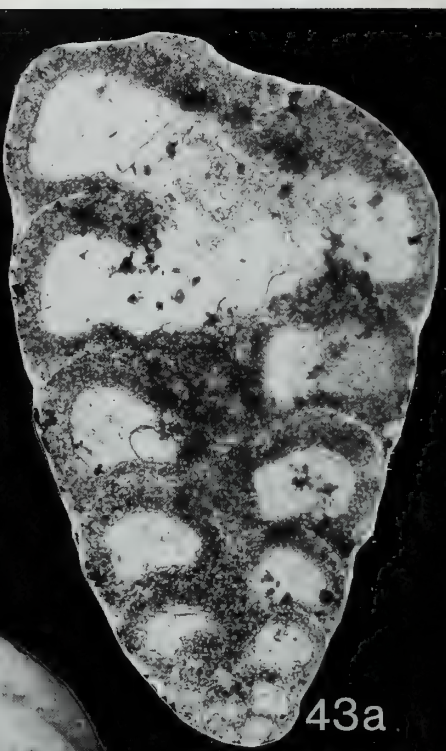
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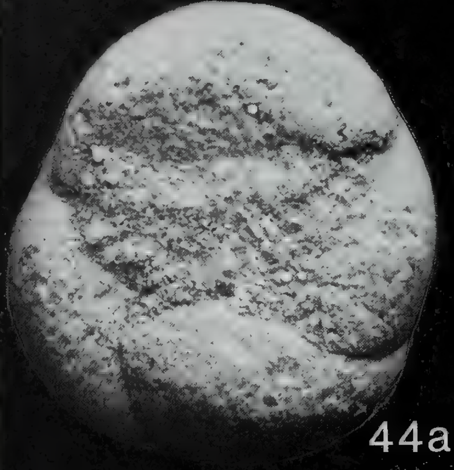
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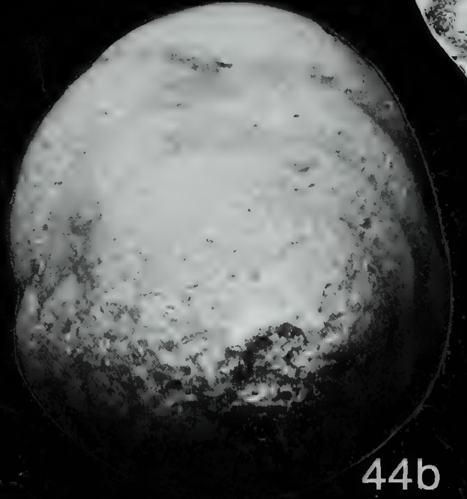
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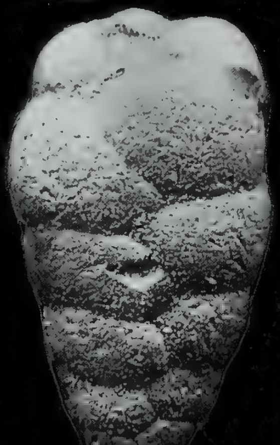
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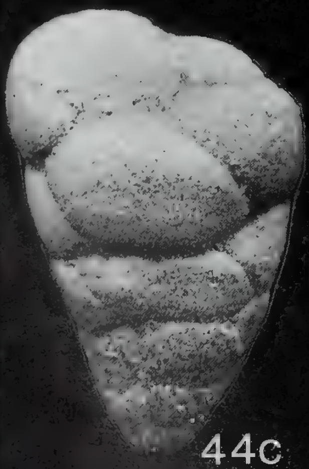
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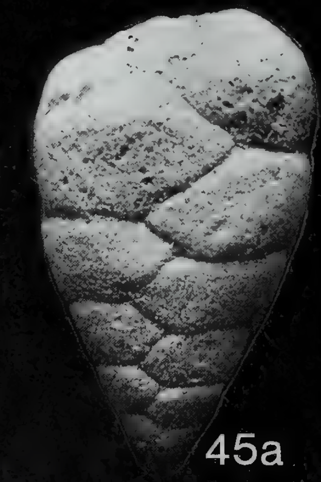
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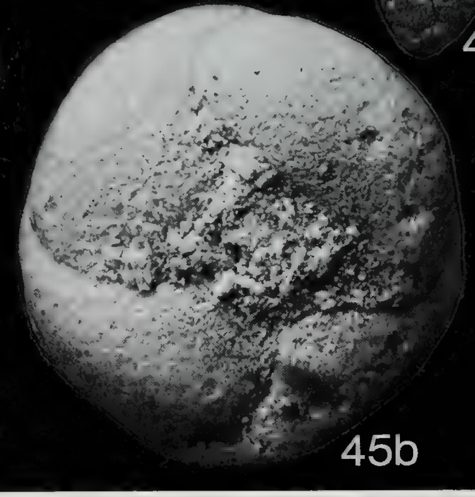

45b

walls. Externally, the intercameral sutures are shallowly depressed.

The apertural face is low. The interiomarginal, umbilical aperture has a narrow, thin lip. The umbilicus is depressed and empty.

DIFFERENTIATION. This species differs from *Redmondoides medius* (Redmond) principally by its slender, slowly tapering test and its partially doubled septa. It is otherwise morphologically very similar to *R. medius* and to *Riyadhoides mcclurei* (Redmond), from which it differs in its terminally quadriserial (not triserial) test.

REMARKS. Redmond (1965) noted that *Redmondoides primitivus* occurred at stratigraphically older levels than *Riyadhoides mcclurei*; it is probable that *Redmondoides primitivus* was ancestral to both *Riyadhoides mcclurei,* which gained terminal triseriality, and to *Redmondoides medius*, which broadened the cone and probably gave rise to the other forms of *Redmondoides* and thence to *Pseudomarssonella* and its descendants.

PROVENANCE OF TYPES. The holotype and two paratypes were obtained by Redmond (1965) from Riyadh Water Well 1 (24°37′45″N, 46°41′06″E) at 2400–2410 ft depth, middle Dhruma Formation.

STRATIGRAPHY. This is the oldest named species of *Redmondoides*; it was reported by Redmond (1965) to occur from the uppermost part of the Lower Dhruma formation ('Upper Bajocian?') to the lower part of the Middle Dhruma ('Bathonian'). These are the intervals named by Powers (1968) 'Unit 4' (the Dhibi Limestone Member, the *Ermoceras* Zone of the uppermost Lower Dhruma) and 'Unit 5' (the *Thambites* Zone of the lowest Middle Dhruma); but they were relabelled as 'Units D2 and D3' by Enay *et al.* (1987), who referred both to the late Bajocian. We know of no reliable records of this species from beds proved to be younger than Bajocian.

Redmondoides rotundatus (Redmond, 1965)

Figs 42–45, 79

1965 *Riyadhella rotundata* Redmond: 140: pl. 1, figs 36–39.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present; the walls are initially solid, but become protocanaliculate and, ultimately, canaliculate with growth. The test is quadriserial; it is subcircular in equatorial section, with intercameral sutures weakly and very narrowly depressed, producing a smooth, not lobulate, axial profile. The test initially tapers at 55°–60°, but this reduces to 30° or less (becoming nearly parallel-sided) in the adult, as the chambers enlarge less rapidly.

The chambers are about twice as broad as high, and constitute the outer 40% of the test diameter; the central 20% of the equatorial diameter is umbilical. The terminal face of each chamber is about as thick as the (lateral) wall, but the intercameral septa, being composed of two layers (the terminal wall of a chamber plus the initial, basal wall of the next, succeeding chamber) is nearly twice as thick; even then, the double-thickness septum is less than a quarter as high as the adjacent chambers. The terminal faces of the chambers (and the preceding intercameral septa) are weakly convex, making distinct angles (initially less that 90°, terminally slightly more than 90°) with the chamber walls.

The apertural face is low and convex; the interiomarginal, umbilical aperture is furnished with a thin, narrow, apertural lip. The umbilicus is deep and empty.

REMARKS AND DIFFERENTIATION. The chambers of this species are exceptionally high (appearing nearly square in axial thin section), and it was probably for this reason that Redmond (1965) referred it to *Riyadhella*. However, the holotype and all the paratypes are terminally quadriserial, with distinct angularity between the terminal faces of the chambers and their lateral walls, clearly distinguishing it from that genus. Redmond (1965: 140) said of this species that 'most individuals have four chambers in the final whorl; only a few show a reduction to three chambers.' As stated above, none of the deposited specimens show such a reduction.

In axial thin section, the very thick intercameral septa are additional guides to identity.

STRATIGRAPHY. The holotype and paratypes were obtained from the Riyadh Water Well 1 (24°37′45″N, 46°41′06″E), 2020–2030 ft depth, from beds referred by Redmond (1965) to the Middle Dhruma Formation; he believed that the species was 'common throughout [the] upper part of the Middle Dhruma Formation, Bathonian'. In Powers (1968) the species was recorded as characteristic of the uppermost Middle Dhruma (Unit 8), the *Dhrumaites* Zone limestones and shales, 'Middle or Upper Bathonian', an interval which Enay *et al.* (1987) called 'D6' and referred to the mid/late Bathonian.

Redmondoides rotundatus is known, in random thin section, from beds as young as the Diyab Formation, Oxfordian (Fig. 79, p. 141), from subsurface sequences drilled off-shore at Qatar.

Redmondoides lugeoni (Septfontaine, 1977)

Figs 46–54, 78

1966	Valvulinids indet.; Bayliss: 176; pl. 52, figs 9–10.
1977	*Valvulina lugeoni* Septfontaine: 612–613; fig. 6; pl. 2, figs 2–5.
1977	*Valvulina lugeoni* Septfontaine; Furrer & Septfontaine: 723–724; pl. 2, figs 8–10.
1981	*Valvulina lugeoni* Septfontaine; Septfontaine: 182, 184; pl. 2, fig. 11.
1984	*Valvulina lugeoni* Septfontaine; Pélissié, Peybernès & Rey: 481–482; pl. 2, fig. 13.
1988	*Valvulina lugeoni* Septfontaine; Septfontaine: 248.

Figs 42–45 *Redmondoides rotundatus* (Redmond), from Saudi Arabia, Riyadh Water Well-1, 2020–2030 ft depth, Middle Dhruma Formation, mid or late Bathonian. Figs 42a–b, holotype AMNH FT-1292; a, axial view (length 440 µm), × 150; b, terminal view, × 230. Figs 43a–b, paratype, now sectioned, AMNH FT-1293A; a, axial section (length 450 µm), × 215; b, original axial view (original length 450 µm), × 150. Figs 44a–c, paratype AMNH FT-1293B; a, terminal view, × 200; b, initial view, × 200; c, axial view (length 420 µm), × 145. Figs 45a–b, paratype AMNH FT-1293C; a, axial view (length 380 µm), × 170; b, terminal view, × 270.

Description emended. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present. In thin section, there are very thin innermost and outermost layers of the walls and septa which are optically denser, and appear darker, than the principal, main thickness (analogously to the inner and outer tectoria of some Fusulinina); this could be due to the inner and outer linings of the walls and septa being composed of exceptionally small micrograules adjacently to their inner and outer surfaces. In the main mass of the walls and septa of early chambers, the calcareous microgranules appear to be randomly arranged, but in later chambers they may become protocanaliculate, and, in the last-formed chambers, canaliculi are developed regularly between these alignments.

The trochospiral test is quadriseral throughout much or all of its ontogeny. It is subcircular in equatorial section; in axial section it is subconical in shape, initially tapering at about 70°–80°, but later this appears to reduce to 30°–40° as the chambers enlarge less rapidly. The chambers are about three times as broad as high. The septa are composed of the terminal face of a chamber with the addition of the basal layer of the next, succeeding chamber: the basal layer is a quarter (or less) as thick as the preceding terminal face. In total, the septa are about a quarter to a third as thick as the chambers are high. The chambers constitute the outer third of the test diameter; the central third of the equatorial diameter is umbilical. The aperture is interiomarginal, umbilical and slit-like, being covered by a broad, plate-like lip; the lip is initially as thick as the septum from which is arises, but it thins rapidly away from the aperture which it covers; it then extends over the central, umbilical, third of the test equatorial diameter. Both the septa and the apertural lip are convex, but the latter is relatively strongly depressed, so that the umbilical area of the terminal faces of the test is in a marked depression.

Remarks. In thin sections (Figs 47, 54), kindly sent to us by M. Septfontaine, of limestone samples obtained by him from the type level and locality of *'Valvulina' lugeoni*, the species is clearly seen to be quadriserial in the adult. This coiling mode, alone, excludes it from the Cenozoic, fully triserial genus, *Valvulina*. The walls of true *Valvulina* are also fully canaliculate; these strict topotypes of *Redmondoides lugeoni* (Septfontaine) also show the canaliculation of the walls of the last-formed chambers and the solid walls of earlier ones – the intermediate chambers, though still solid, showing the linearity of the constituent granules which we term 'protocanaliculation' (Figs 48, 51).

Stratigraphic distribution. The type specimens were obtained by Septfontaine (1977) from the Grange Chavan, Préalpes valaisannes, SW of Chablais (Haute-Savoie, France), in the upper part of the 'Couches à *Mytilus*' of Bathonian–Callovian age (Baud *et al.* 1989: 372). Furrer & Septfontaine (1977) recorded the species from sediments precisely dated as Upper Bathonian (and also possibly older) in an adjacent region. Septfontaine (1988: 238, 248) later believed *'Valvulina' lugeoni* to have its first stratigraphic appearance in the Lower Dogger (in the Bajocian, and possibly even in the Aalenian) in the Mesogean Realm. We have found it in beds probably as old as Bajocian (the Izhara Formation) drilled subsurface, off-shore Abu Dhabi (Fig. 78, p. 141). In the Préalpes briançonnaise, the Callovian marine sediments are closed by a major, regional disconformity (Baud *et al.* 1989), and this may be responsible for the absence of post-Callovian records of *Redmondoides lugeoni* in that area.

Conspecific specimens were illustrated by Bayliss (1966) from the Bau Limestone Formation of western Sarawak, a formation which also contained *Pseudocyclammina maynci* Hottinger (illustrated by Bayliss and recorded by him as '*P. lituus* (Yokoyama) form α Maync'), a species which also occurs in the 'couches à *Mytilus*' of the Préalpes (Hottinger 1967), as well as in beds believed to range Callovian–Oxfordian in the High Atlas of Morocco (Brun 1963). However, the Bau Limestone was also found to contain *Torinosuella peneropliformis* (Yabe & Hanzawa) and *Pseudocyclammina lituus* (Yokoyama) (Bayliss 1966), suggesting that the formation ranges up into the Kimmeridgian; therefore, the youngest occurrences here of *Redmondoides lugeoni* may also be as young as this.

Genus ***RIYADHOIDES*** nov.

Type species. *Pseudomarssonella mcclurei* Redmond, 1965.

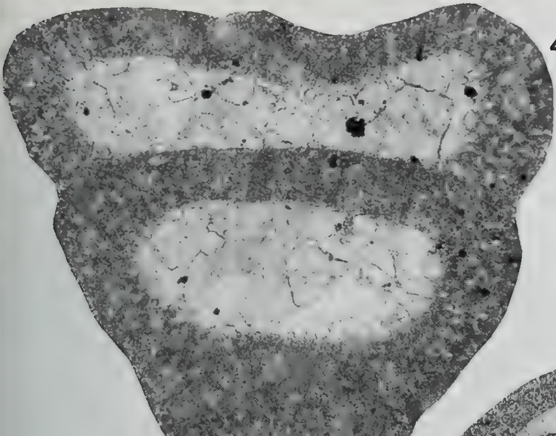
Diagnosis. A chrysalidinid with an initially quadriserial test reducing to adult triseriality; adult primary aperture interiomarginal, central in position; no apertural flap, no umbilicus or internal, umbilical pillars, no areal, accessory apertures; terminal faces and septa are flattened.

Name. From Riyadh, capital city of Saudi Arabia.

Remarks. As in *Riyadhella*, the triserial terminal whorls of *Riyadhoides* consist of chambers so closely appressed that no umbilical space can exist between them. This applies not only to the slender tests of *R. mcclurei* but also to the conical, more rapidly tapering tests of *R. dumortieri* (Schwager), which has been clearly illustrated from the Kimmeridgian – Lower Tithonian by Riegraf & Luterbacher (1989: pl. 2, figs 1–8).

The reduction during ontogeny in the number of chambers

Figs 46–54 *Redmondoides lugeoni* (Septfontaine), metatypic topotypes, random thin sections in micritic limestone, sample Se785, from the upper part of the *Mytilus* Beds, Bathonian or Callovian, at Grange Chavan, Préalpes valaisannes, near Chablais, Haute-Savoie, France. Fig. 46, BMNH P 52610, off-centred axial section (length 600 μm), showing canaliculi in walls and septa (with protocanaliculation in the umbilical area), × 110. Fig. 47, BMNH P 52612, equatorial section (breadth 1300 μm), showing partially protocanaliculate or canaliculate chamber walls, × 45. Fig. 48, BMNH P 52613, axial section (length 1260 μm), × 70. Fig. 49, BMNH P 52614, off-centred axial section (length 1280 μm), showing protocanaliculate or canaliculate terminal septum and the final, basal layer separating from its underlying (penultimate) septum, × 45. Fig. 50, BMNH P 52615, axial section, slightly oblique (length 1400 μm), × 35. Fig. 51, BMNH P 52616, axial section (length 2030 μm), showing broad, plate-like, apertural lips, × 35. Fig. 52, BMNH P 52611, axial section (length 620 μm), × 80. Fig. 53, BMNH P 52617, off-centred, axial section of terminal whorls (breadth 910 μm), showing canaliculate chamber walls and solid septa, × 75. Fig. 54, BMNH P 52618, equatorial section (breadth 1260 μm), showing quadriseriality and partially protocanaliculate chamber walls, × 45.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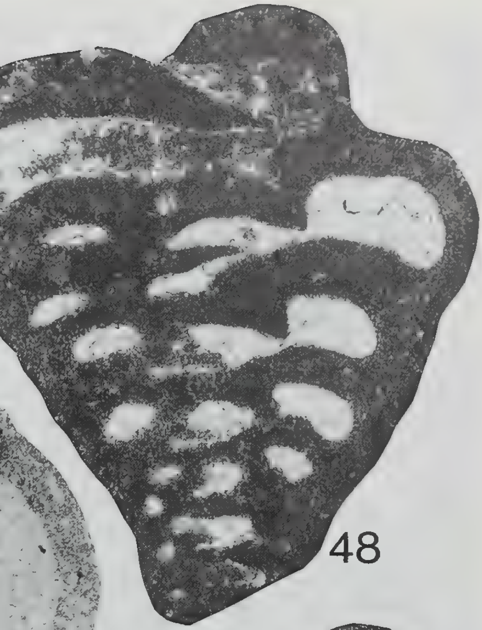
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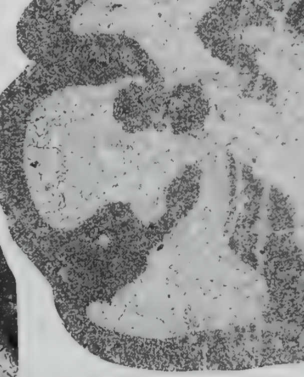
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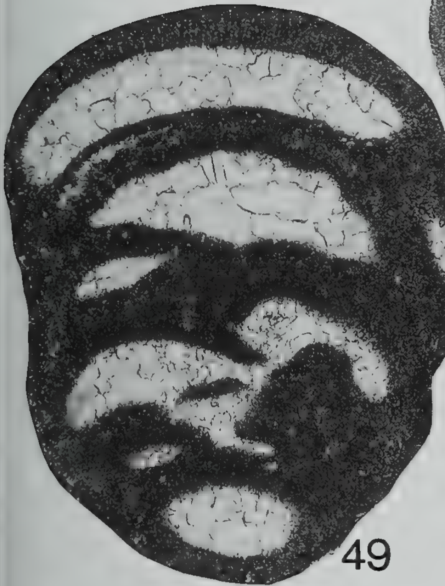
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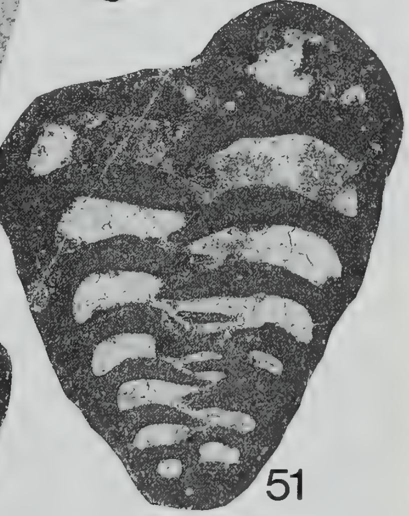
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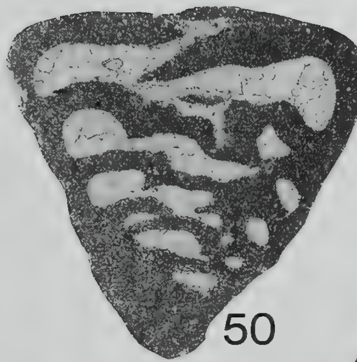
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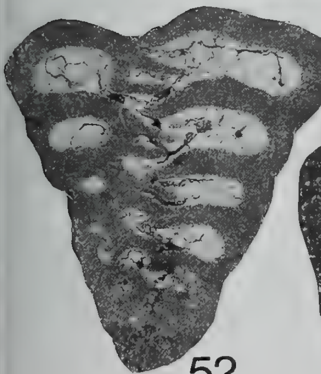
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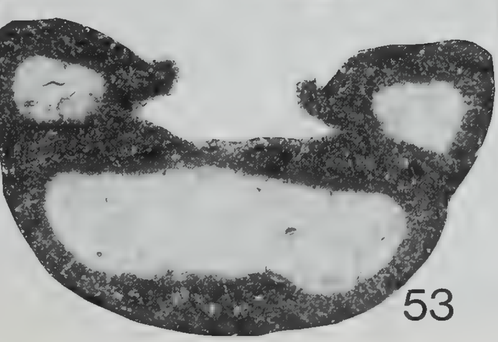
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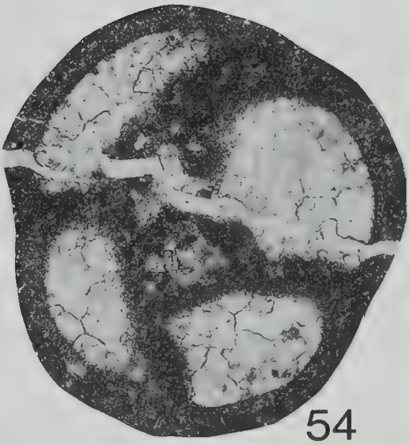
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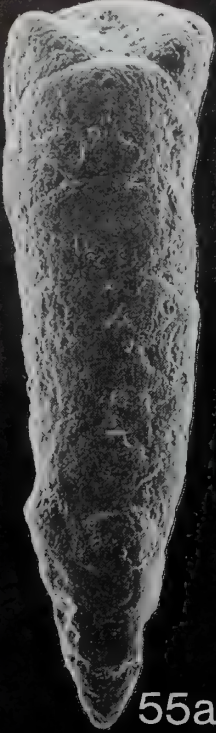
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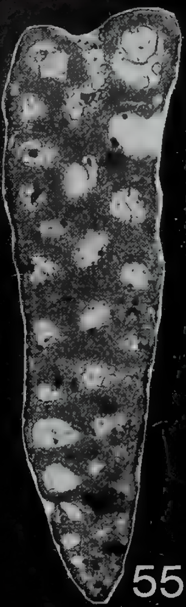
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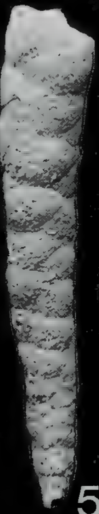
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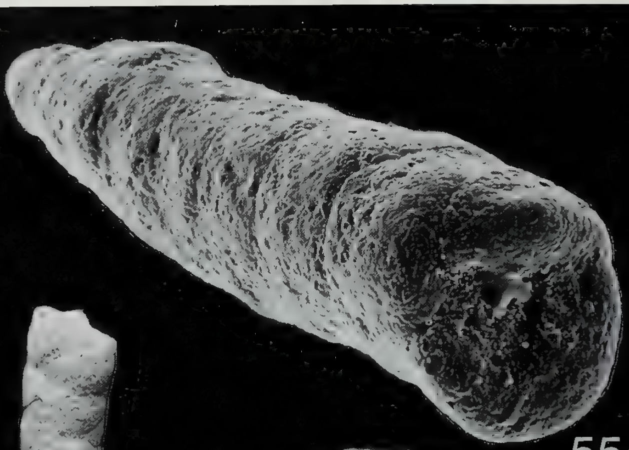
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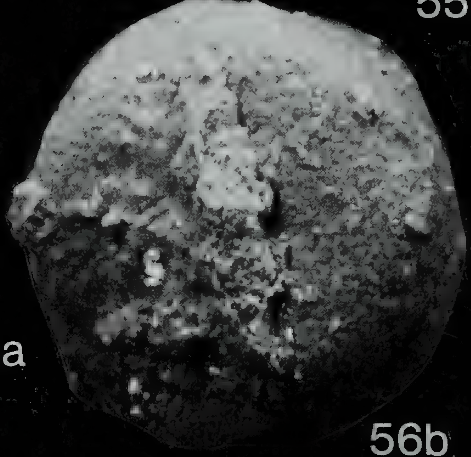
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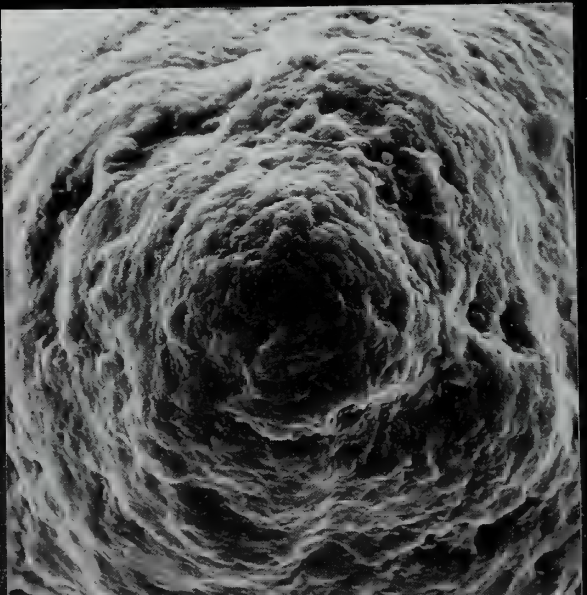
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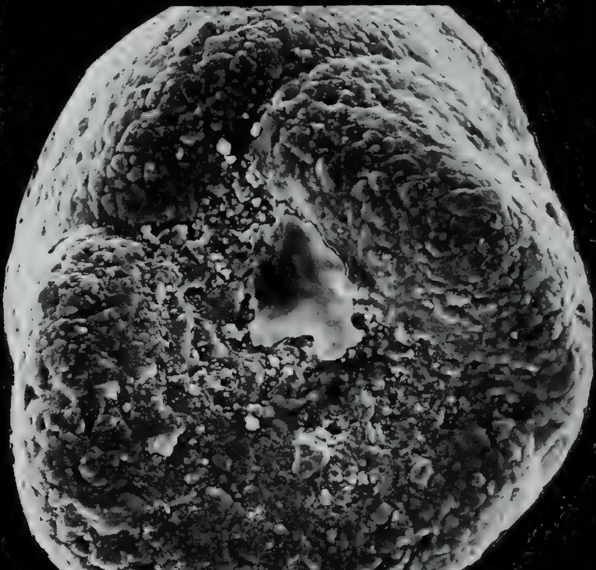
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er whorl may be so great that the test can approach iseriality; however, true biseriality is not achieved. It is ossible, but cannot yet be demonstrated, that further reduc- ion in terminal chamber numbers, to achieve true biseriality, volved *Protomarssonella* Desai & Banner near the beginning f the Cretaceous.

IFFERENTIATION AND AFFINITY. *Redmondoides*, presumed ncestor of *Riyadhoides*, differs in its quinqueserial–quadriserial oiling, as well as in possessing an umbilicus over which pertural flaps may develop. *Riyadhoides* differs from *Proto-* *arssonella* in lacking terminal biseriality. It may be distin- uished easily from *Riyadhella* Redmond by its flattened rminal faces (and septa), which form distinct angles with the ninflated chamber walls.

iyadhoides mcclurei (Redmond, 1965) Figs 55–56

965 *Pseudomarssonella mcclurei* Redmond: 135; pl. 1, figs 8–10.

ESCRIPTION EMENDED. Test calcareous, microgranular, with o known canaliculi or protocanaliculate structure. The initial uadriserial part of the test is tapering, but the adult triserial art is slender, subcylindrical and nearly parallel-sided. The amber walls are uninflated and the intercameral sutures are nly narrowly and shallowly depressed. The intercameral epta are virtually perpendicular to the chamber wall, as the rminal faces of the septa are flattened or are only very ightly convex. The interiomarginal, slit-like aperture is tuated in a deep re-entrant in the high apertural face and is ntrally placed, in the margin of a narrow, empty umbilicus.

ROVENANCE OF TYPES. The type specimens were obtained by edmond (1965) from the Riyadh Water Well 180 (24°37′27″N, °41′40″E) at 2421–2431 ft depth (ditch sample), Middle hruma Formation.

TRATIGRAPHY. Believed by Redmond (1965) to be rare in the wer part of the Middle Dhruma Formation, the species was ferred by him to the Bathonian. Powers (1968) recorded the ecies as characterizing a zone in the lowest unit (Unit 5), e *Thambites* Zone limestone, of the Middle Dhruma ?Lower Bathonian'), but Enay *et al.* (1987) called this unit 3' and assigned it to the latest Bajocian.

Genus ***RIYADHELLA*** Redmond, 1965

YPE SPECIES. *Riyadhella regularis* Redmond, 1965.

72 *Eomarssonella* Levina: 101 (type species *E. paraconica* Levina, 1972)

88 *Pseudoeggerella* Septfontaine: 246 (type species *P. elongata* Septfontaine, 1988).

IAGNOSIS. A chrysalidinid with an initially quinqueserial or adriserial test, reducing to adult triseriality; primary aper- re interiomarginal, central in position; no apertural flap, no nbilicus or internal, umbilical pillars; no areal, accessory ertures; terminal faces and septa are convex.

REMARKS. The adult reduction to triseriality in *Riyadhella* results in the production of tests which are terminally very slowly tapering or even parallel-sided. They differ from the similarly-shaped *Riyadhoides* in their highly convex septa (and chamber terminal faces) which have no trace of angularity at the junction between them and the adjacent chamber walls.

Redmond's species of *Riyadhella* were known to him only as solid specimens from the Late Bajocian and Bathonian of Saudi Arabia. Some of these specimens have now been sectioned (Figs 57–58, 63) and can be directly compared with the published photographs of the type specimens of *Pseudoeggerella* Septfontaine, which was known only as random thin sections of specimens in microfossiliferous, Bathonian limestones of Switzerland. Septfontaine (1988: 246) believed that adult *Pseudoeggerella* was quinqueserial, but neither the holotype of the type species (originally figured by Septfontaine, 1980: pl. 1, fig. 12) nor the paratypes (figured by him in 1988) suggest this to us. The 'small protuberances' in the middle part of the sectioned chambers, also considered by Septfontaine (1988) to be significant, we ascribe to partial sections of a third (or, in the earlier test, fourth) chamber of each whorl. The 'narrow columella in the axis of the test', also mentioned by Septfontaine (1988), we believe to consist of the innermost walls of the adjacent chambers, cut slightly away from the plane of the central axis (see Fig. 58c herein); there is no umbilical axial space in the test of this genus. Therefore, we believe that *Riyadhella* and *Pseudoeggerella* are synonymous, and we also consider that *P. elongata* Septfontaine is a junior synonym of *R. regularis* Redmond. In consequence, the genera may be regarded as subjective typonyms and *Riyadhella elongata* (Septfontaine, 1988) becomes a junior synonymous homonym of *R. elongata* Redmond, 1965.

Eomarssonella paraconica Levina, the type species of that genus, was described and figured by Levina (1972: pl. 32, figs 1–11; see also those figures reproduced by Loeblich & Tappan, 1988: pl. 140, figs 9–12) from the Oxfordian of western Siberia. Although some specimens (e.g. Levina 1972: pl. 32, fig. 1a) may have abnormally inflated chambers in the last whorl only, the shape of the earlier test (like the complete tests of other specimens) is indistinguishable from typical *Riyadhella*; the megalospheric form has four chambers in each early whorl, reducing to adult triseriality, the septa are highly and smoothly convex, and there is no open umbilicus. It is possible that *R. paraconica* is a junior synonym of *R. inflata* Redmond, or is, at least, closely related to it.

DIFFERENTIATION AND AFFINITY. *Riyadhella* differs from *Redmondoides* gen. nov. by its highly convex chambers, in which the terminal faces and lateral walls blend in a smooth curve with no angular junction, in its adult triseriality and in its lack of an umbilicus. It differs from *Verneuilinoides* Loeblich & Tappan by its initial quadriseriality.

STRATIGRAPHY. Named species of *Riyadhella* are known from late Bajocian (*R. elongata* Redmond), to Callovian (e.g. '*R. hemeri*' Redmond, considered to be a synonym of *R. regularis*

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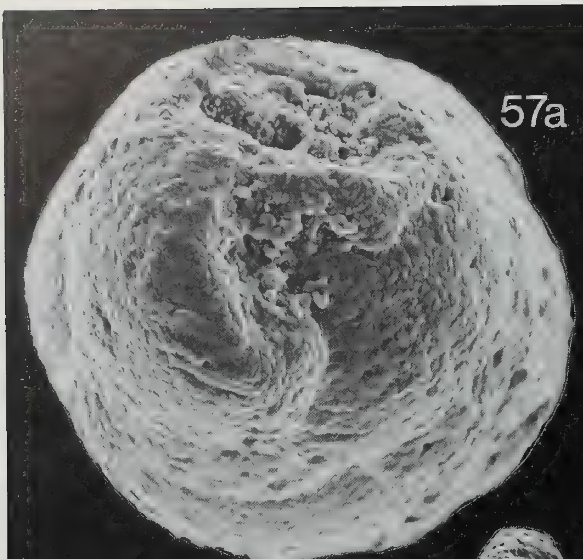
gs 55–56 *Riyadhoides mcclurei* (Redmond), from Saudi Arabia, Riyadh Water Well-180, 2421–2431 ft depth, Middle Dhruma Formation, uppermost late Bajocian. Figs 55a–e, paratype AMNH FT-1272, now sectioned; a, original axial view (length 500 µm), × 200; b, axial section, × 160; c, oblique terminal view, × 250; d, initial view, × 2000; e, terminal view, × 600. Figs 56a–b, holotype AMNH FT-1271; a, axial view (length 940 µm), × 70; b, terminal view, × 600.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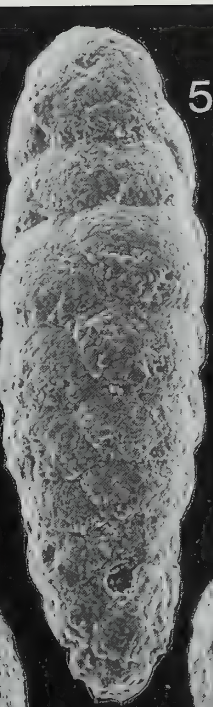
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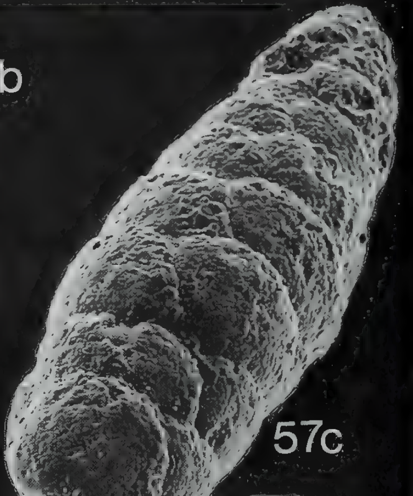
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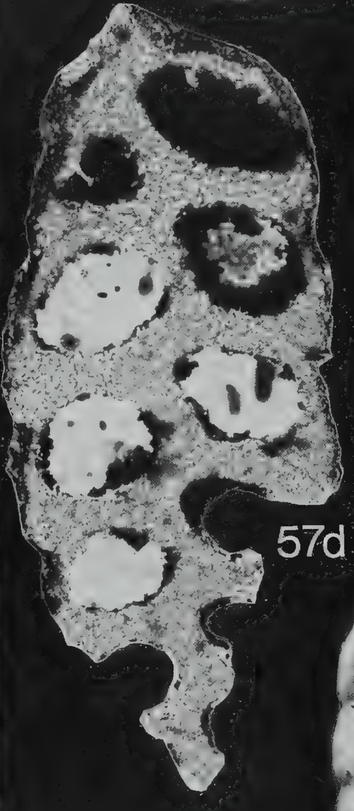
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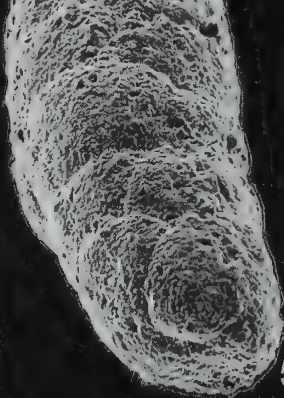
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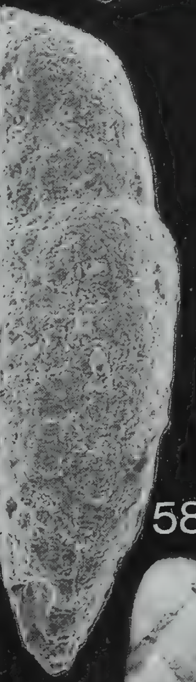
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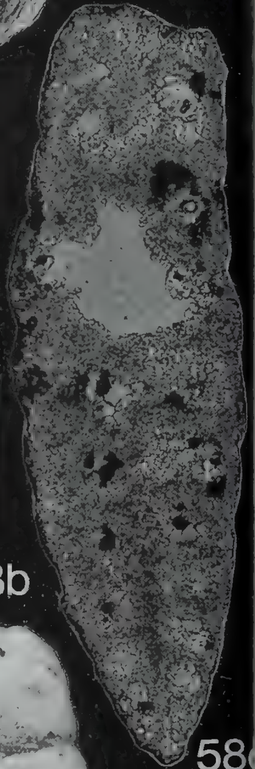
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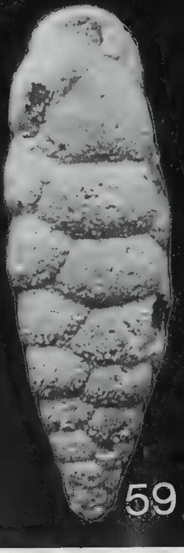
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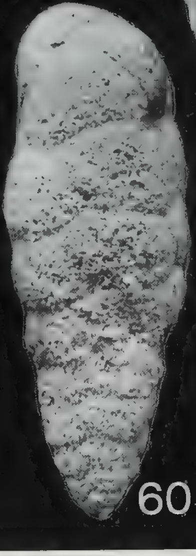
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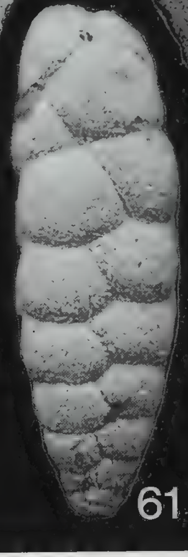

61

Redmond) and to Oxfordian (*R. paraconica*). Unnamed species of *Riyadhella* are known to us, in random thin section, in the Kimmeridgian Arab Zone ('C' Zone) limestone of Qatar. The genus is known only from the mid and late Jurassic, and so differs from its presumed ancestor, *Verneuilinoides*, which ranges from early Jurassic to Cretaceous.

Riyadhella regularis Redmond, 1965 Figs 57–63

965 *Riyadhella regularis* Redmond: 138–140; pl. 1, figs 32–34.
965 *Riyadhella hemeri* Redmond: 137; pl. 1, figs 23–24.
965 *Riyadhella intermedia* Redmond: 137–138; pl. 1, figs 25–27.
965 *Riyadhella nana* Redmond: 138; pl. 1, figs 28–31.
980 '*Pseudoeggerella*' Septfontaine: 181–182; pl. 1, fig. 12.
988 *Pseudoeggerella elongata* Septfontaine: 246; pl. 2, figs 6–8.

DESCRIPTION EMENDED. Walls and septa of microgranular calcite, with little or no adventitious agglutinated material; no protocanaliculation or canaliculi are known. The nepionic est is quadriserial, but the neanic and ephebic parts of the est are regularly triserial. The test is subcircular in cross-ection; in axial view, the test initially tapers at about 5°–40° but soon becomes approximately parallel-sided. The hambers are about as high as broad, but those of successive whorls embrace the preceding ones for about a third to half of heir height. The intercameral sutures are weakly depressed; he surfaces of both walls and terminal faces are smooth. The erminal faces of the chambers (and the septa of earlier hambers) are highly convex. In longitudinal section, the hickness of each septum is about a quarter of the total height f its chamber. The apertural face is low, flattened but therwise ill-defined, containing a deep re-entrant depression n which is situated the narrow, short, interiomarginal, slit-ke aperture.

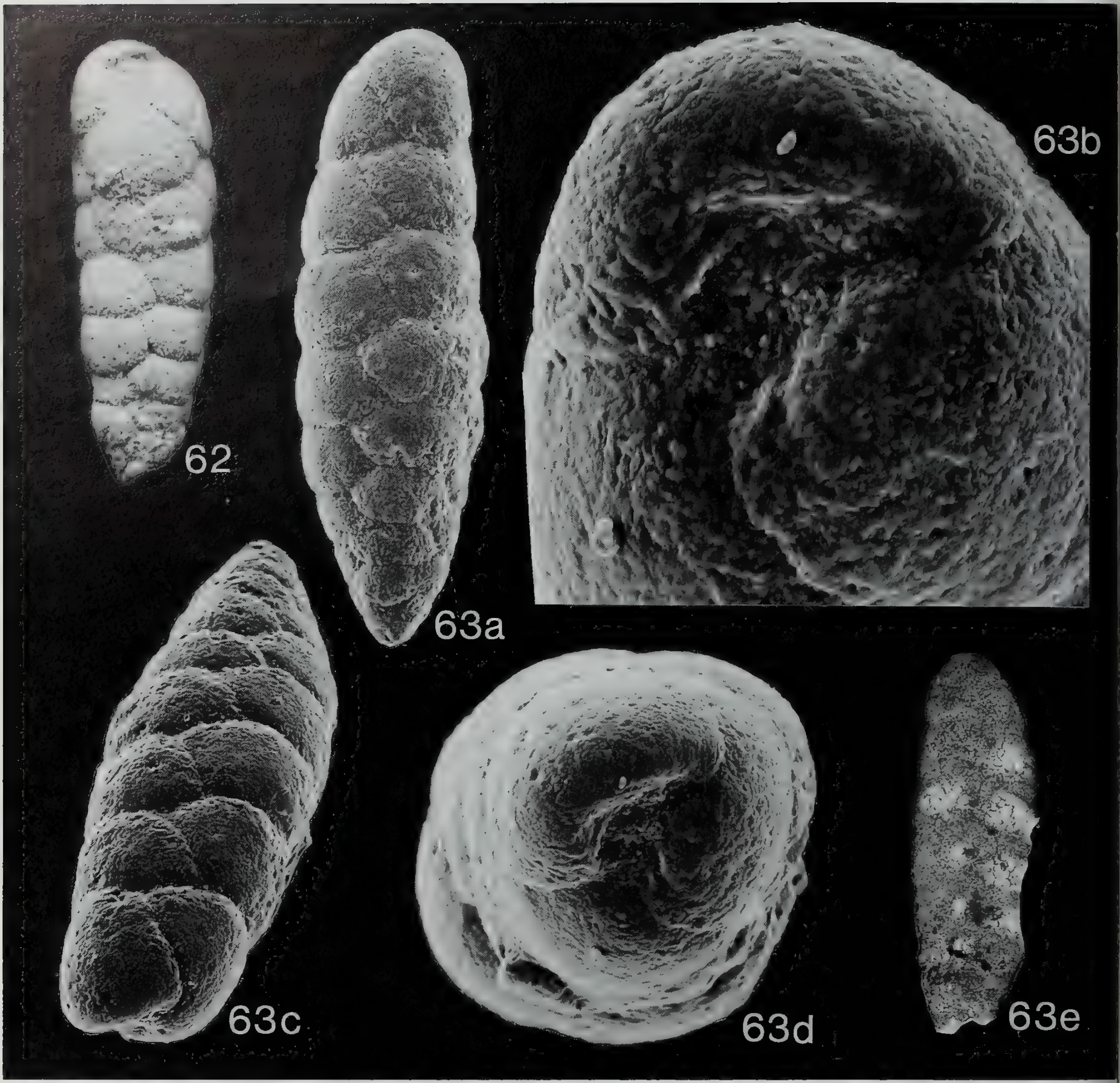
REMARKS. Redmond (1965) considered that the test of *Riyadhella regularis* had an initial part which was more longately conical than the 'blunter' initial end of *R. intermedia*. Neither Redmond's published pictures (1965: pl. 1, gs 25–27 and 32–34) nor our SEM images (Figs 57–60) ubstantiate this. Also, Redmond (1965) considered that hese taxa had 'relatively straight sides', while *R. nana* and *R. emeri* were distinguished by being broader medially, the ormer having its widest diameter closer to its 'apex' than in he latter. The test of *Riyadhella* is often broadest at the last uadriserial whorls (the succeeeding triserial whorls being ften, but not always, slimmer); the relative position in the est of this event depended on the extent of triserial chamber growth which had been achieved. These differences are both minor and unsystematically developed. Consequently, we consider all these taxa to be synonyms, and (by ICZN Art. 24) as first revisers we select *R. regularis* (designated by Redmond, 1965, as the type species) to have priority.

DIFFERENTIATION. *Riyadhella regularis* Redmond is much broader than *R. elongata* Redmond, a species which also remains quadriserial for at least half of the length of its elongate test: in *R. regularis*, quadriseriality is retained only for a quarter, or less, of the length of the adult test. *R. arabica* Redmond and *R. inflata* Redmond are broader and more tapering and have more broadly inflated chambers.

PROVENANCE OF TYPES. The type specimens of *Riyadhella regularis* (Figs 57, 59) came from Aramco well T 60A (24°55′04″N, 45°59′08″E), 40–60 ft depth, basal member of the Upper Dhruma Formation. Of the synonyms, the *R. nana* type specimens (Figs 62–63) came from the same well, but from 100–105 ft depth, the upper part of the Middle Dhruma Formation. The holotype (there were no paratypes) of *R. hemeri* (Fig. 61) came from Aramco surface locality (outcrop) C-3 (24°12′48″N, 46°21′20″E), 'shale approximately 51 metres below the base of the cliff-forming limestone of the Tuwaiq Mountain Formation' (Redmond 1965: 140), which Powers (1968) referred to the Hisyan (Hishyan) Member of the uppermost Dhruma Formation. The type specimens of *R. intermedia* (Figs 58, 60) were obtained from the same shale member, about 25 m below the Tuwaiq Mountain Formation limestone, at Aramco surface (outcrop) locality L 930A (sample 32) (24°10′50″N, 46°27′53″E).

STRATIGRAPHY. *Riyadhella nana* was obtained primarily from beds referred by Powers (1968) to the *Dhrumaites* Zone, 'Unit 8' of the uppermost Middle Dhruma, beds which were relabelled 'D6' by Enay *et al.* (1987) and considered by them to be mid or late Bathonian. *R. regularis* was recorded as 'common in the basal member of the Upper Dhruma' (Redmond 1965) which was called the 'Atash Member ('Unit 9') by Powers (1968); Enay *et al.* (1987), who called the member 'D7a', considered it to be late Bathonian or early Callovian in age, but they had no direct palaeontological evidence. *R. hemeri* and *R. intermedia*, from the Hisyan Member ('D7b') were mid Callovian by the stratigraphy of Enay *et al.* (1987), who also considered the overlying Tuwaiq Mountain Formation to be mid Callovian in age. The species is therefore known to range from mid or late Bathonian to mid Callovian, and Septfontaine's specimens (1980, 1988) are believed to have come from the Bathonian part of this range.

gs 57–61 *Riyadhella regularis* Redmond, from Saudi Arabia. Figs 57a–d, paratype of *R. regularis* AMNH FT-1291, now sectioned; from Aramco Well T 60A, 40–60 ft depth, basal Upper Dhruma Formation, 'Atash Member, late Bathonian or early Callovian; a, terminal view, × 600; b, axial view (length 360 μm), × 250; c, oblique axial view, × 300; d, axial section, × 385. Figs 58a–c, paratype of the synonymous *R. intermedia* Redmond, AMNH FT-1287, now sectioned; from Aramco outcrop L 930A, Hisyan Member, Upper Dhruma Formation, mid Callovian; a, oblique axial view, × 250; b, axial view (length 460 μm), × 200; c, axial section, × 225. Fig. 59, holotype of *R. regularis* AMNH FT-1290, from same sample as paratype (Fig. 57); axial view (length 420 μm), × 165. Fig. 60, holotype of the synonymous *R.intermedia* Redmond, AMNH FT-1286, from the same sample as its paratype (Fig. 58); axial view (length 440 μm), × 160. Fig. 61, holotype of the synonymous *R. hemeri* Redmond, AMNH FT-1283, from Aramco outcrop C-3, Hisyan Member, Upper Dhruma Formation, mid Callovian; axial view (length 450 μm), × 155.



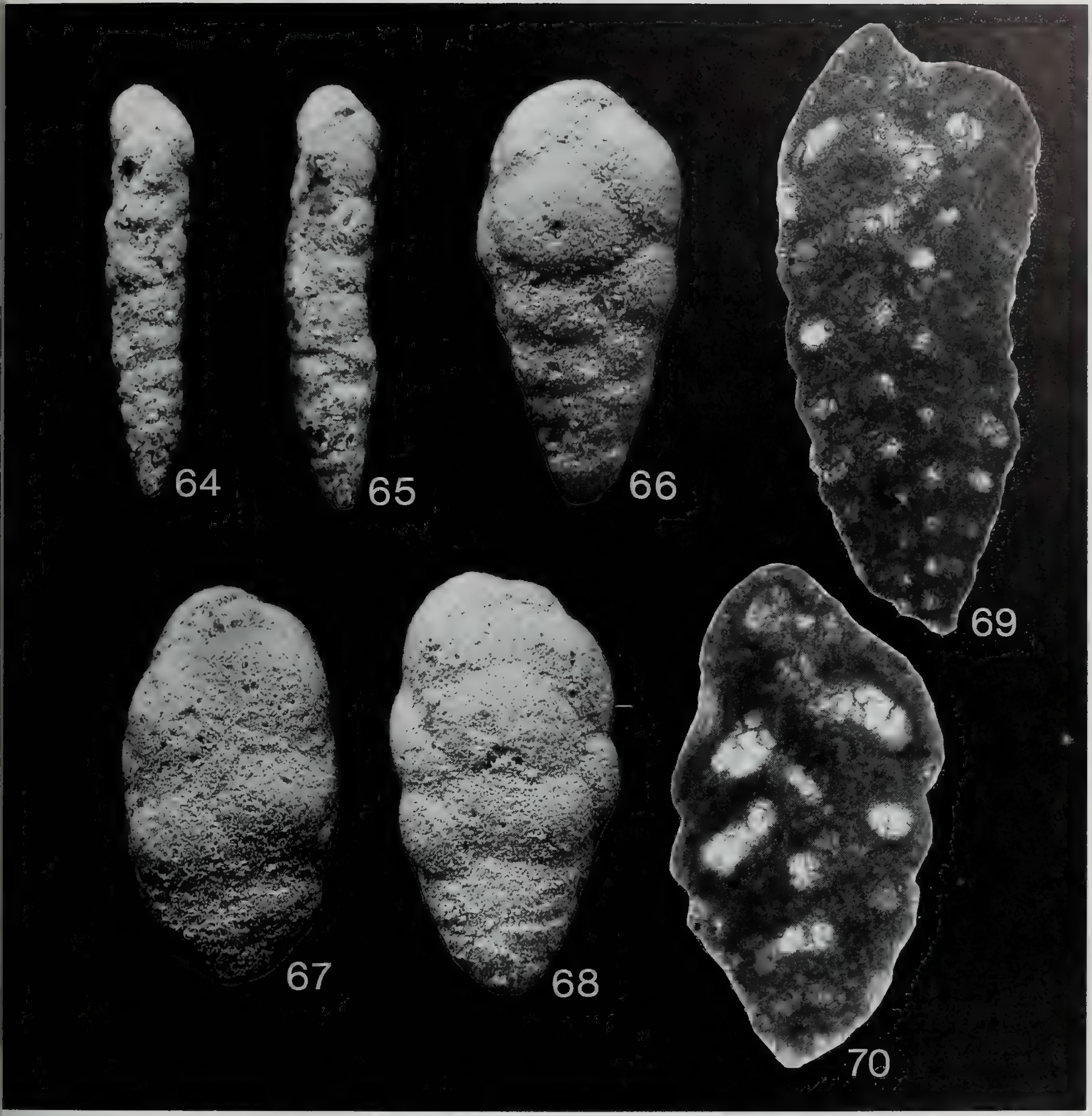
Figs 62–63 *Riyadhella regularis* Redmond; primary types of the synonymous *R. nana* Redmond, from Saudi Arabia, Aramco Well T 60A, 100–105 ft depth, upper Middle Dhruma Formation, mid or late Bathonian. Fig. 62, holotype of *R. nana*, AMNH FT-1288; axial view (length 370 μm), × 190. Figs 63a–e, paratype of *R. nana*, AMNH FT-1289, now sectioned; a, original axial view (length 390 μm), × 250; b, apertural view, × 1,000; c, oblique axial view, × 300; d, terminal view, × 500; e, axial section, × 160.

Riyadhella arabica Redmond, 1965 Fig. 66

1965 *Riyadhella arabica* Redmond: 136; pl. 1, fig. 35.

Remarks. Only the holotype of this taxon was deposited by Redmond in the American Museum of Natural History, so the species cannot properly be redescribed. Also, the aperture is obscured on the holotype by a coating of calcareous sediment. However, the holotype is much bigger than the specimens referred here to *R. regularis*, more broadly tapering (initially at about 40°–45°) and does not clearly become parallel-sided in the adult. The chambers are smooth-walled, weakly inflated, and are about as high as broad; successive whorls embrace previous ones by about half the chamber height. *R. inflata* Redmond has much higher chambers, and in that species successive whorls embrace previous ones by about a quarter of the chamber height.

The type specimen of *R. arabica* Redmond came from Riyadh Water Well 1, at 2355–2360 ft depth – the same sample as that from which the type specimens of *R. elongata* Redmond were obtained – and Redmond (1965) reported



igs 64–65 *Riyadhella elongata* Redmond, from Saudi Arabia, Riyadh Water Well-1, 2350–2360 ft depth, Middle Dhruma Formation, early Bathonian. Fig. 64, holotype AMNH FT-1281, axial view (length 450 μm), × 145. Fig. 65, paratype AMNH FT-1282, axial view (length 440 μm), × 150.

ig. 66 *Riyadhella arabica* Redmond, from Saudi Arabia, Riyadh Water Well-1, 2355–2360 ft depth, Middle Dhruma Formation, early Bathonian; holotype AMNH FT-1280, axial view (length 400 μm), × 170.

igs 67–68 *Riyadhella inflata* Redmond, from Saudi Arabia, Aramco Well T 80, 60–70 ft depth, Middle Dhruma Formation, mid or late Bathonian. Fig. 67, holotype AMNH FT-1284, axial view (length 610 μm), × 110. Fig. 68, paratype AMNH FT-1285, axial view (length 610 μm), × 110.

igs 69–70 *Riyadhella* spp. from Iraq, Wadi Amij Well, depth 570–573 ft (same locality and depth as for the holotype of *Amijiella amiji* (Henson); called '?*Verneuilina* sp.' by Henson, MS), probably Bathonian, Muhaiwir Formation. Fig. 69, BMNH P 52619, axial section (length 690 μm), × 140. Fig. 70, BMNH P 52620, axial section (length 560 μm), × 140.

that this species was 'rare in the middle and lower parts of [the] middle Dhruma Formation'. Enay *et al.* (1987) would refer this interval to the early Bathonian.

It is possible that *R. arabica* Redmond is a distinct species, as its holotype appears to be morphologically distinct from the type specimens of the other taxa, and Redmond's (1965) treatment may prove to have been correct.

Riyadhella elongata Redmond, 1965 Figs 64–65

1965 *Riyadhella elongata* Redmond: 136–137; pl. 1, figs 20–21.

Description emended. Walls and septa of microgranular calcite, with scattered fine quartz particles in the walls, which roughen the chamber surfaces; no protocanaliculation or canaliculi are known. The nepionic and neanic parts of the test are quadriserial but triseriality is attained in the ephebic stage. The test is subcircular in cross-section; initially, it tapers at about 30° but it becomes parallel-sided and slender during late quadriseriality and this is maintained during triseriality, so that the adult test is $4\frac{1}{2}$–5 times as long as broad. The chambers are about as high as broad, but those of successive whorls embrace the preceding ones for about a third to half of their height. The intercameral sutures are distinctly depressed, and the walls are inflated; the terminal faces are highly convex. The apertural face is low, and the short, interiomarginal aperture is set in a broad re-entrant depression.

Differentiation. *Riyadhella elongata* Redmond is easily recognized by its thin, parallel-sided test, which Redmond (1965) called 'needle-like', and its ontogenetically late development of triseriality.

Provenance of types. The type specimens were obtained from the Riyadh Water Well 1 (24°37′45″N, 46°41′06″E) at 2350–2360 ft depth, Middle Dhruma Formation.

Stratigraphy. Redmond (1965) reported that *R. elongata* first occurred in the 'uppermost part of [the] lower Dhruma', an occurrence recorded by Powers (1968) who placed it in his 'Unit 4', the Dhibi Member (*Ermoceras* Zone) of the Lower Dhruma; this was relabelled 'Unit D2' by Enay *et al.* (1987), who believed it to belong to the earliest late Bajocian. These are the stratigraphically earliest records yet of *Riyadhella*. Redmond (1965) also believed *R. elongata* to be 'rare in middle and lower part of middle Dhruma Formation', occurrences which were noted by Powers (1968) in his 'Unit 6' (*Tulites* Zone) and 'Unit 7' (*Micromphalites* Zone) of the middle Middle Dhruma; Enay *et al.* (1987) renamed these units 'D4' and 'D5' and believed both to comprise the Lower Bathonian. Therefore, *R. elongata* is believed to range from the earliest Late Bajocian to the latest early Bathonian.

Riyadhella inflata Redmond, 1965 Figs 67–68

1965 *Riyadhella inflata* Redmond: 137; pl. 1, figs 23–24.
?1972 *Eomarssonella paraconica* Levina: 102–104; pl. 32, figs 1–11.

Description emended. The test is of microgranular calcite (with little or no adventitious agglutinated material) with a smooth surface; no protocanaliculation or canaliculi are yet known. The nepionic test is quadriserial, but triseriality is achieved in the neanic and ephebic stages. The test is subcircular in cross-section. In axial view, the test initially tapers broadly (at about 70°) and then more narrowly (at about 50°), becoming nearly parallel-sided in the adult. The chambers are about as high as broad, and those of successive whorls embrace those of preceding whorls by a quarter, or less, of their height. The chamber walls are weakly inflated and the intercameral sutures are distinctly and smoothly depressed. The terminal faces are highly convex. The apertural face is very low, and slightly flattened and oblique to the longitudinal axis of the test; the short aperture is interiomarginal and set at the base of a narrow, shallow depression in the apertural face.

Differentiation. The test is much larger (thicker and proportionately longer) than any other known species of *Riyadhella*, and its chambers are higher and less embraced by succeeding whorls. The chambers are more evenly inflated, and the intercameral sutures are more smoothly, more evenly depressed. *R. paraconica* (Levina) is very similar in general morphology but its walls may be built with more adventitious, agglutinated, terrigenous material; its identity with *R. inflata* Redmond should be checked by direct re-examination of the type specimens.

Provenance of types. The type specimens of *R. inflata* Redmond came from Aramco well T 80 (24°10′50″N, 46°27′ 53″E), from 60–70 feet depth, a level ascribed (Redmond 1965) to the Middle Dhruma Formation.

Stratigraphy and distribution. Stated by Redmond (1965) to be 'common in upper part of [the] middle Dhruma Formation', *R. inflata* was recorded by Powers (1968) from the top unit ('Unit 8'), the *Dhrumaites* Zone, of the Middle Dhruma, 'middle or upper Bathonian'. Enay *et al.* (1987) renamed the unit 'D6', but also considered that it was mid or late Bathonian in age. It has not yet been recorded from any other interval.

The type specimens of *R. paraconica* (Levina) came from the Lower Oxfordian near Tyumen' (57°11′N, 65°29′E), western Siberia, and it was also recorded (Levina 1972) from the Upper Oxfordian of that region. This is the most northerly known occurrence of *Riyadhella*, and, if its synonymity with *R. inflata* is proved, it shows that that species is the longest ranging (Bathonian–Oxfordian).

Genus ***PSEUDOMARSSONELLA*** Redmond, 1965

Type species. *Pseudomarssonella maxima* Redmond, 1965.

Diagnosis emended. A chrysalidinid with a test which is initially quinqueserial or quadriserial, then either retaining quadriseriality throughout ontogeny or developing quinqueseriality in the ephebic stage of development; the adult

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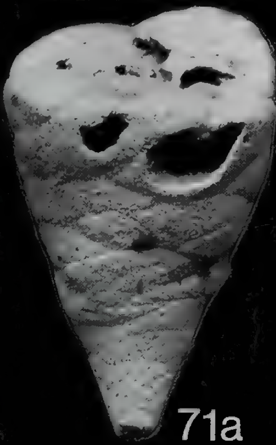
Fig. 71 *Pseudomarssonella maxima* Redmond, holotype AMNH FT-1269, from Saudi Arabia, Aramco well T 60A, 50–60 ft depth, basa Upper Dhruma Formation ('Atash Member), late Bathonian or early Callovian; a, axial view (length 630 μm), × 95; b, axial-terminal view showing canaliculate wall, × 350; c, terminal view, × 155; d, enlargement of part of last whorl (of Fig. 71a), showing canaliculi in broken chamber wall, × 475; e, apertural terminal view, × 325.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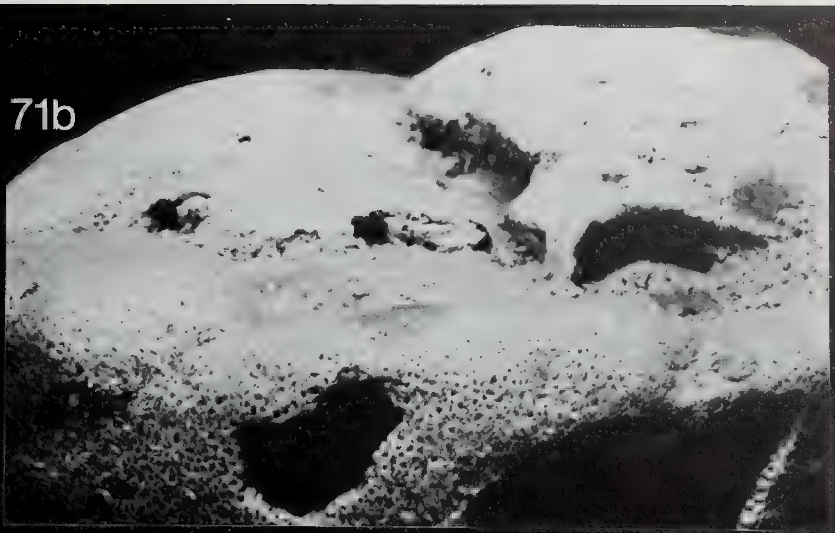
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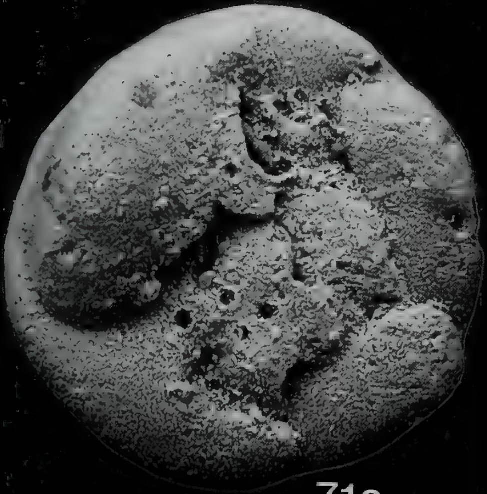
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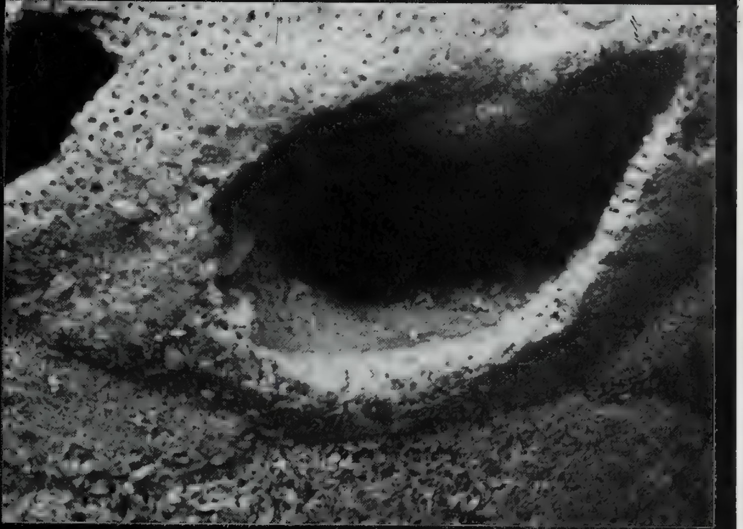
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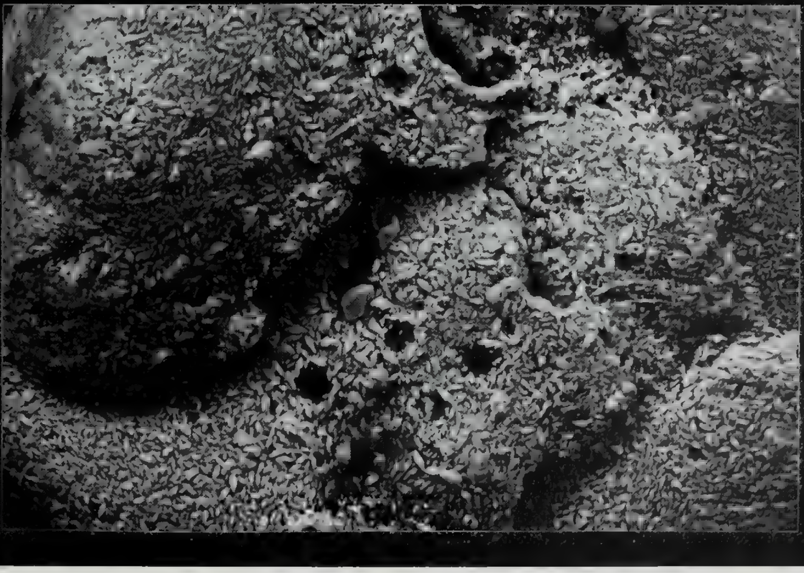
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primary, interiomarginal aperture is covered by an apertural flap which fuses to the apertural flap or face of an opposing chamber, and which is penetrated by areal, accessory, cribrate, pore-like apertures; the apertural flaps of successive whorls are closely appressed and can fill the deep umbilical hollow with a layered column of successive flaps; there are no internal, umbilical pillars; the terminal faces and septa are flattened or only weakly convex, and make distinct angles with the uninflated chamber walls.

Remarks and differentiation. The broadening of the umbilicus and umbilical hollow (compared to the narrower structure in *Redmondoides*) led to the broadening of the apertural flap and its strengthening by fusion with the surface of opposite chambers; this fusion caused loss of the interiomarginal accessory aperture and its replacement by areal accessory apertures. The increased breadth of the umbilicus led to five chambers (rather than the ancestral four) being able to surround it in some species. Successive flaps became closely appressed (even when only four chambers occupied the whorl – the acquisition of five chambers per whorl would have meant that five, not four, flaps would have been accommodated in each whorl), and cytoplasm, egressing from the chamber lumina through the areal, cribrate apertures,

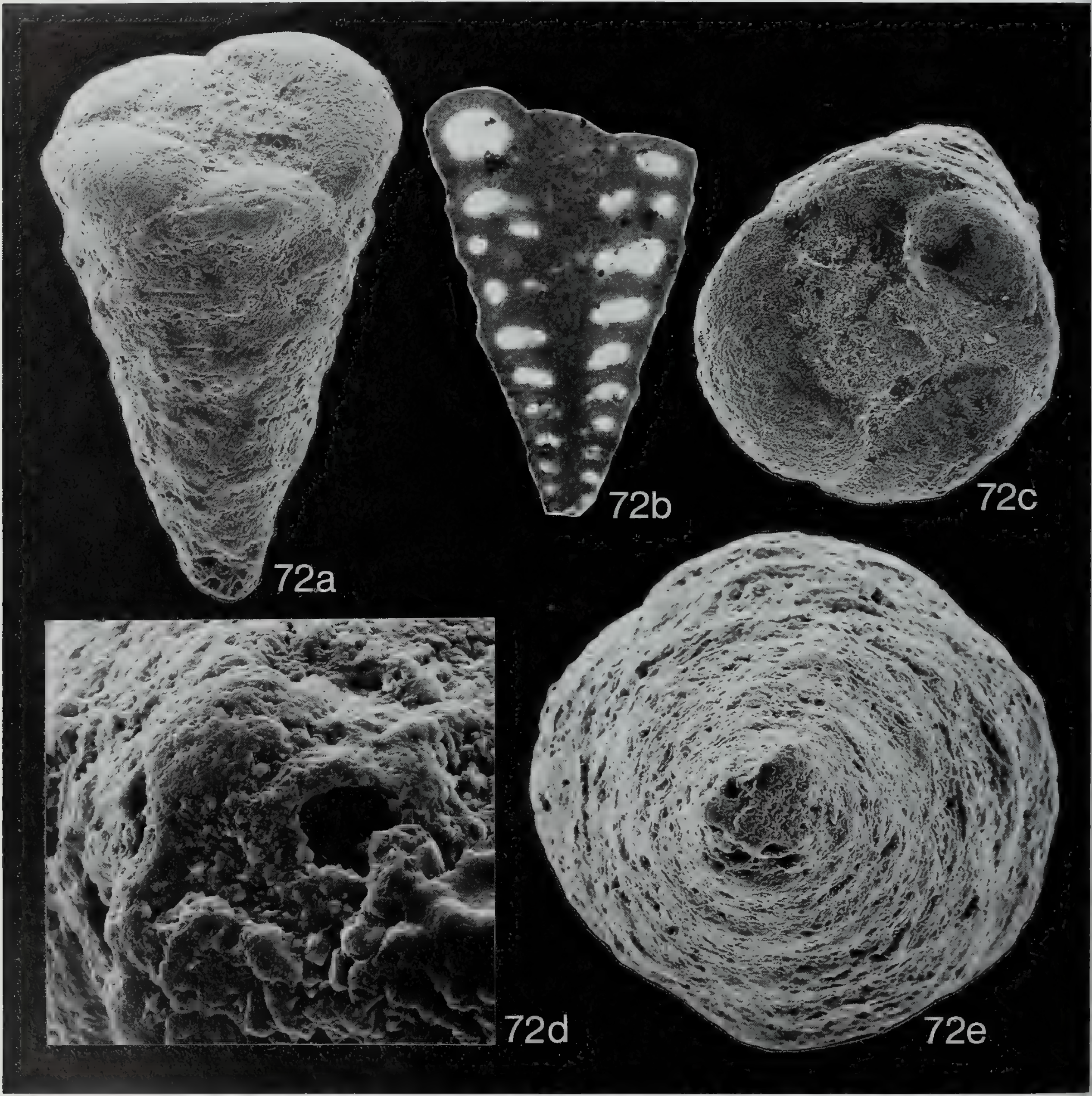


Fig. 72 *Pseudomarssonella maxima* Redmond, paratype AMNH FT-1270, from same locality and sample as holotype (Fig. 71, p. 135), now sectioned; a, original axial view (length 600 µm), × 150; b, axial section, × 115; c, terminal view, × 150; d, initial end, × 1,100; e, initial view, × 220.

would have had narrow, sheet-like channels to traverse, between the successive flaps. This may have encouraged the development of the succeeding *Paravalvulina*, where inter-flap spacing was enlarged and structural support was provided by the development of inter-flap pillars.

SPECIES INCLUDED AND STRATIGRAPHY. In addition to *Pseudomarssonella maxima* Redmond, the type species, three other nominal species, named by Redmond (1965), are retained in the genus: *P. bipartita* and *P. plicata* (with the subjective synonym of the latter, *P. reflexa*). These are redescribed below, and the revised known range for the genus is regarded as mid Bathonian to mid Callovian (following the revision of the stratigraphy by Enay *et al.*, 1987). No species firmly assignable to this genus have yet been described from deposits of western Tethys and it is so far known only from Saudi Arabia and from offshore wells of Qatar and the United Arab Emirates.

Pseudomarssonella maxima Redmond, 1965 Figs 71–72

1965 *Pseudomarssonella maxima* Redmond: 135; pl. 1, figs 6–7.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material; the calcite microgranules are random in early ontogeny, but they become aligned and the walls become protocanaliculate until canaliculi can develop in the final growth stages, both in chamber walls and septa. The test may be quinqueserial nepionically but it rapidly becomes quadriserial, sometimes becoming quinqueserial again, in the final growth stage. It is subcircular in cross-section and axially it is a regularly tapering cone, with its sides diverging at about 40°.

The intercameral sutures are very narrowly and gently depressed or are flush with the chamber walls. The walls are uninflated and the terminal faces and septa are weakly convex, making angles of 90° or more with the walls; the angular wall–septal junctions sometimes project very slightly rom the test sides. The chambers are about twice as broad as high.

The interiomarginal, umbilical primary apertures are covered by broad, flattened or slightly convex flaps which span most or all of the umbilicus to fuse with the flaps or apertural faces of opposing chambers. The flaps are penetrated by areal, cribrate, pore-like accessory apertures, each of which is circular and is usually furnished with a narrow, low, upstanding rim. The umbilical area is slightly concave, the umbilical laps being flatter than, originating below and being depressed below the terminal faces of the last-formed chambers. In ongitudinal section, the flaps of successive whorls of chambers are closely appressed, being separated by spaces no hicker than (and sometimes much thinner than) the flaps hemselves. The umbilicus broadens with growth, becoming rom 35% to 55% of the equatorial diameter of the test.

REMARKS. Only the holotype and one paratype were deposited by Redmond in the American Museum of Natural History. In order to redescribe this taxon as fully as possible, he paratype was first photographed by SEM (Figs 72a, c–e), and then longitudinally sectioned and re-photographed (Fig. 2b). The total lack of internal, intraumbilical (inter-flap) pillars serves now to distinguish *Pseudomarssonella* Redmond rom *Paravalvulina* Septfontaine, taxonomically and phylogenetically.

DIFFERENTIATION. *Pseudomarssonella maxima* differs from *P. plicata* Redmond in possessing a much broader umbilicus, with broader apertural flaps, and less depressed chamber walls and much less protruding mural–septal junctions. *P. maxima* differs from *P. bipartita* Redmond in having more convex, less flattened septa and terminal faces and in being less fully quinqueserial terminally. All three species are clearly very closely related and the differences between them may be infraspecific. However, the Aramco records (restated by Powers, 1968) of full microfossil assemblages regarded them as being taxonomically distinct, and it would be unwise to contradict this when using only a few, although type, specimens.

PROVENANCE OF TYPES. The holotype and paratype were obtained by Redmond (1965) from Aramco well (drill hole) T 60A (24°55′04″N, 45°59′08″E), at 50–60 ft depth, basal member of the Upper Dhruma Formation.

STRATIGRAPHY. Redmond (1965) stated that *P. maxima* was 'rare to common throughout basal member of [the] upper Dhruma Formation', and it was cited by Powers (1968) as occurring in the 'Atash (chalky) Member ('Unit 9'). This was relabelled 'D7a' by Enay *et al.* (1987), who considered it to be late Bathonian or early Callovian. The type specimens are therefore younger than those of *P. bipartita* Redmond (mid or late Bathonian), but are of the same age as some of those of *P. plicata* Redmond (early Bathonian to late Bathonian or early Callovian).

Pseudomarssonella bipartita Redmond, 1965 Figs 73–74

1965 *Pseudomarssonella bipartita* Redmond: 134; pl. 1, figs 2–3.

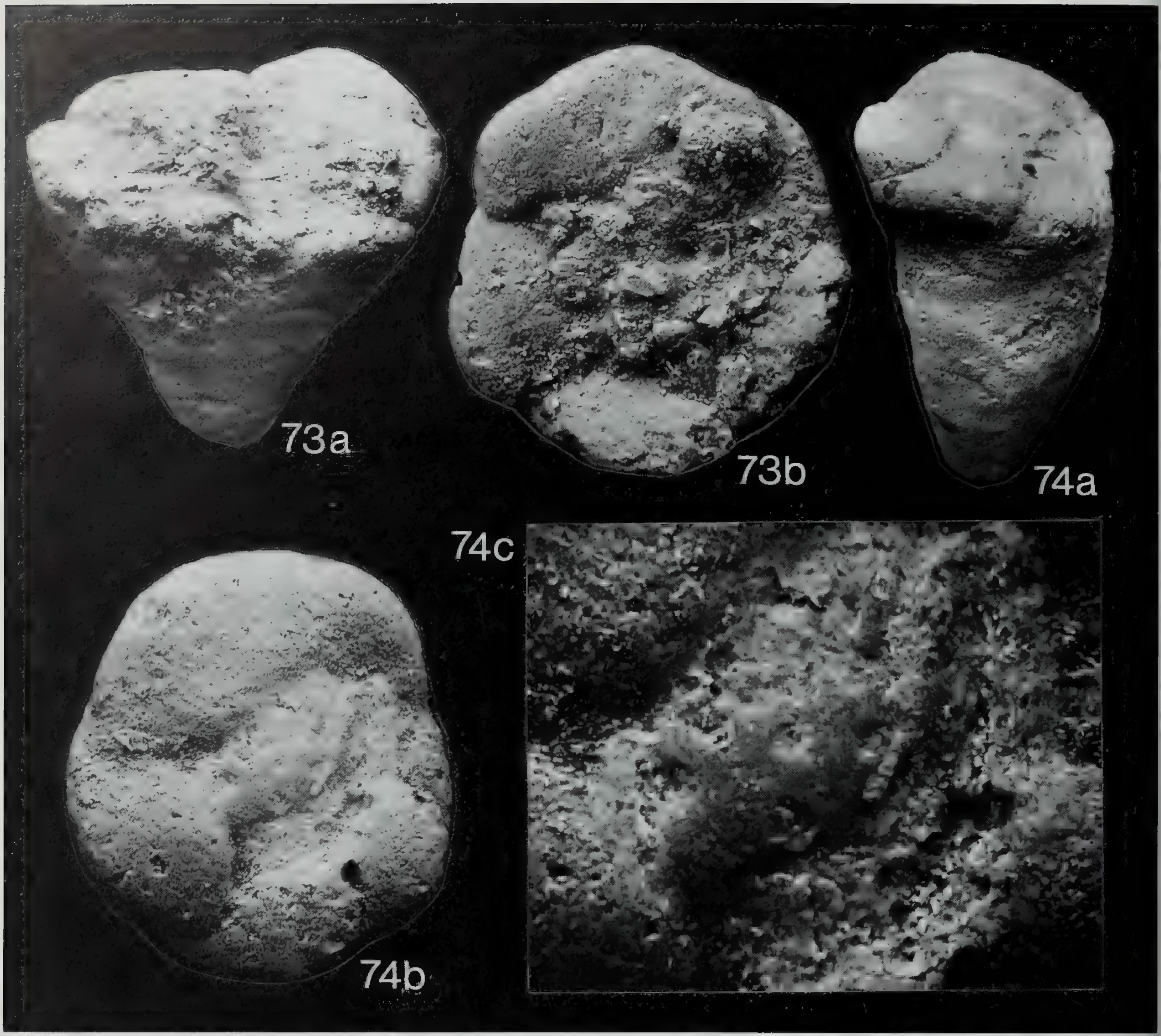
non 1989 *Pseudomarssonella bipartita* Redmond; Delance & Ruget: 206; pl. 3, fig. 16.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material; canaliculi are not yet known. The test may be quinqueserial nepionically, but it becomes, at least neanically, quadriserial and is ephebically and terminally quinqueserial. It is subcircular in cross-section, and axially it is a narrowly or broadly tapering cone, tapering initially at about 40° but terminally maintaining or diminishing this angle (to about 30°) or becoming flaring (to about 70°); in all cases, five chambers constitute the last whorl.

The late chambers are about $2\frac{1}{2}$ times as broad as high and constitute about 30% of the test diameter; the central 40% of the equatorial diameter is umbilical. The terminal faces of the chambers are flattened or very weakly convex, and the chamber walls are uninflated; the intercameral sutures are very narrowly depressed or flush with the chamber walls.

The interiomarginal primary apertures are covered by broad, flattened or very weakly convex flaps which span most or all of the umbilicus, to fuse with the apertural faces or flaps of the opposing chambers. The flaps are penetrated by areal, cribrate, pore-like accessory apertures. The umbilical area is slightly concave, the umbilical flaps being depressed below the terminal faces of the last-formed chambers.

DIFFERENTIATION. *Pseudomarssonella bipartita* Redmond is the only species distinctly to possess five chambers per whorl in its terminal growth stage.

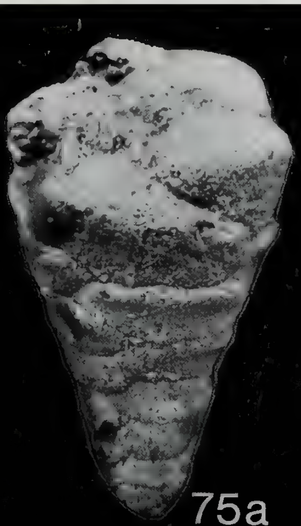


Figs 73–74 *Pseudomarssonella bipartita* Redmond, from Saudi Arabia, Aramco Well T 61, 80–90 ft depth, Middle Dhruma Formation, mid or late Bathonian. Figs 73a–b, holotype AMNH FT-1265; a, axial view (length 440 μm), × 140; b, terminal view, × 140. Figs 74a–c, paratype AMNH FT-1266; a, axial view (length 560 μm), × 110; b, terminal view, × 140; c, apertural area, × 325.

Remarks. The difference in tapering angles between the holotype (Fig. 73a) and paratype (Fig. 74a) cannot be ascribed to structural differences between the megalospheric and microspheric generations because the tapering angles of the initial parts of the tests are the same. In each case, also, the number of chambers per adult whorl is the same. Therefore, the difference must be due to an increased rate of growth (in the case of specimens like the holotype) during ephebic ontogeny, while in others (like the figured paratype) the chamber-enlargement rate remained constant or even diminished. This could have resulted from palaeoecological differences and, therefore, would not have been inherited.

The specimen figured as *P. bipartita* by Delance & Ruget (1989) is referred by us to *Redmondoides medius* (Redmond) (p. 120).

Figs 75–77 *Pseudomarssonella plicata* Redmond. Figs 75–76, primary types; from Saudi Arabia, Aramco Well T 60A, 10–20 ft depth, basal Upper Dhruma Formation ('Atash Member), late Bathonian or early Callovian. Figs 75a–b, holotype AMNH FT-1275; a, axial view (length 410 μm), × 160; b, initial view, × 270. Figs 76a–c, paratype AMNH FT-1276; a, axial view (length 350 μm), × 200; b, terminal view, × 290; c, lateral view of apertural area, × 450. Figs 77a–b, holotype AMNH FT-1279 of the synonymous *P. reflexa* Redmond, from Saudi Arabia, Aramco well 4A, 4875 ft depth, Middle Dhruma Formation, early Bathonian; a, terminal view, × 150; b, axial view (length 560 μm), × 120.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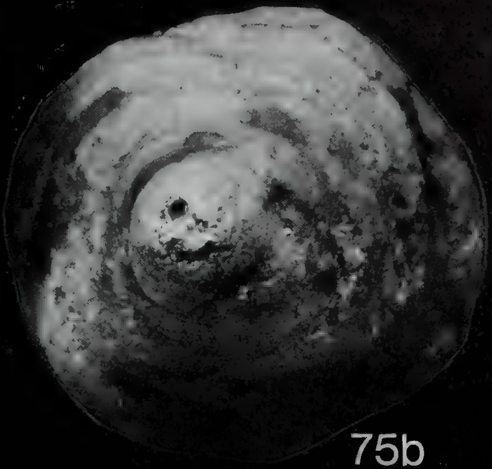
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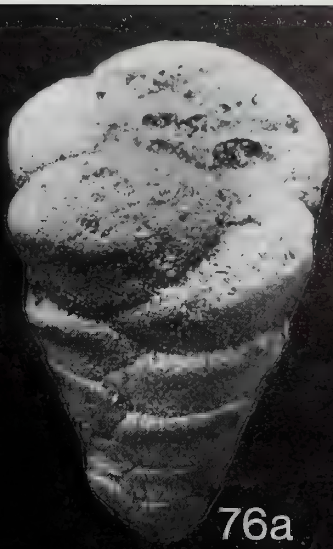
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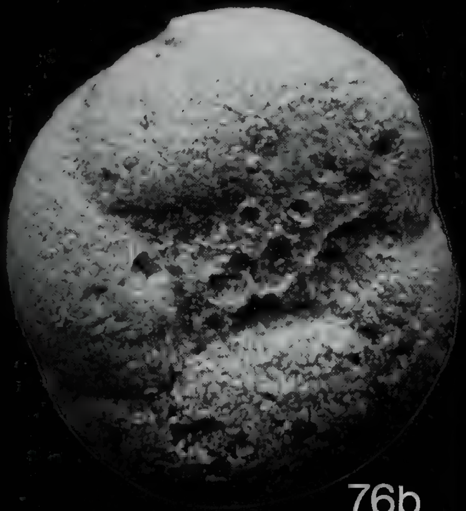
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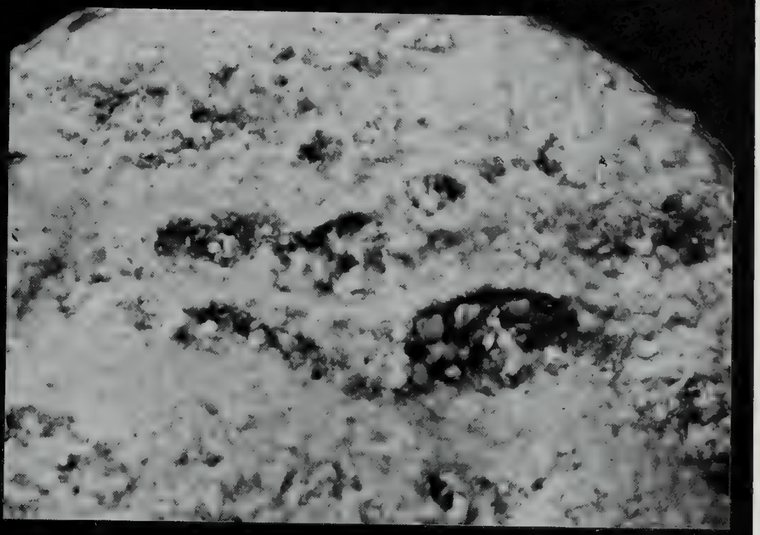
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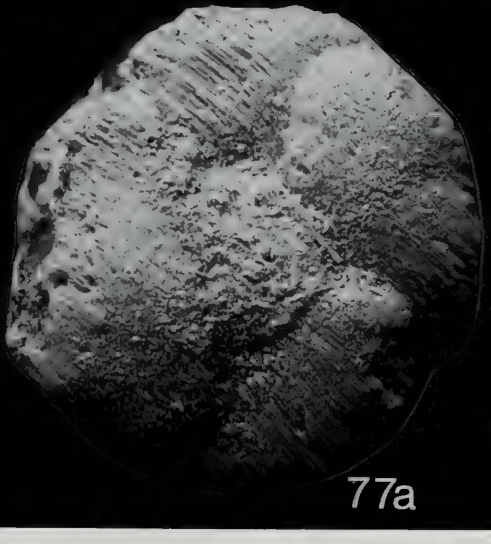
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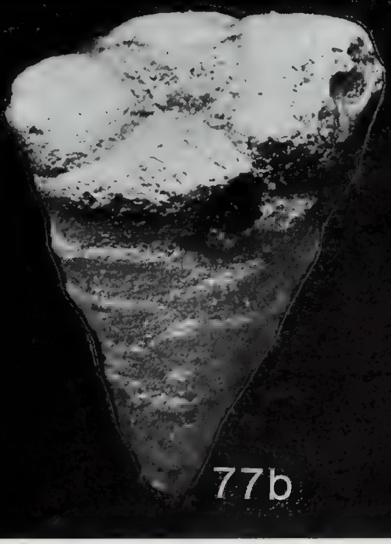
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PROVENANCE OF TYPES. The type specimens of *P. bipartita* came from Aramco well T 61 (24°54′55″N, 45°58′34″E), from 80–90 ft depth, Middle Dhruma Formation.

STRATIGRAPHY. Redmond (1965) recorded *P. bipartita* as being 'rare to common in the upper part of middle Dhruma Formation', and Powers (1968) reported it from Unit 8 (the *Dhrumaites* Zone limestones and shales of the uppermost Dhruma). Enay *et al.* (1987) renamed this unit 'D6' and considered it to belong to the mid or late Bathonian.

Pseudomarssonella plicata Redmond, 1965 Figs 75–77

1965 *Pseudomarssonella plicata* Redmond: 135; pl. 1, figs 14–15.
1965 *Pseudomarssonella reflexa* Redmond: 136; pl. 1, figs 19a–b.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material; canaliculi are not yet known. The test may be quinqueserial nepionically, but it is quadriserial for most, at least, of its growth; it is subcircular in equatorial section, and axially it is conical, tapering steadily at 40°–50°.

The chambers are about three times as broad as high, and constitute the outer 35% of the test diameter; the central 30% of the equatorial diameter is umbilical. The terminal faces of the chambers are only very weakly convex, while the chamber walls are uninflated; the walls and the terminal faces meet at distinct but obtuse angles. The intercameral sutures are flush or very narrowly depressed, but may be marked by the slight protrusion of these angular mural–septal junctions.

The interiomarginal primary apertures are covered by broad flaps which arise from low on the apertural face to extend to and fuse with the lower part of the apertural face of the opposite chamber; the accessory apertures are multiple, cribrate, pore-like and emerge through the area of the flaps; each accessory aperture is subcircular and is bounded by a weakly elevated rim. The umbilical area is slightly concave, the umbilical flaps being depressed below the terminal faces of the last-formed chambers.

REMARKS AND DIFFERENTIATION. This species is morphologically very similar to *Redmondoides medius* (Redmond) in its depressed, slightly concave chamber walls and in the markedly angular junction between them and the terminal faces of the chambers. Its apertural characters are, however, quite distinct from those of *Redmondoides*. *Pseudomarssonella maxima* Redmond differs in possessing a broader umbilical area, with more convex umbilical flaps, in lacking the protrusive mural–septal junctions at the terminal peripheries of the chambers, and in being slightly more slender (tapering at 35°–40°).

Redmond (1965) distinguished *P. reflexa* by its conical test growth, in which the chambers were believed to enlarge more rapidly as ontogeny proceeded, producing an increasing angle of flare in the later test and concave sides to the test as a whole. As only the holotype of this nominal species was deposited by Redmond (there were no paratypes), nothing can be independently and objectively assessed of the constancy of such a morphocharacteristic. However, we can see no difference between this species, as represented by its holotype, and *P. plicata*, and, as first revisers (ICZN Art. 24), we choose the latter to be the senior synonym.

PROVENANCE OF TYPES. The type specimens of *P. plicata* were obtained by Redmond (1965) from Aramco well T 60A (as for *P. maxima*), at 10–20 ft depth, from the basal member of the Upper Dhruma Formation. The type of *P. reflexa* came from Aramco stratigraphic well 4A (27°51′19″N, 44°54′47″E), a core from 4875 ft depth, Middle Dhruma Formation.

STRATIGRAPHY. Redmond (1965) stated that '*P. reflexa* ... [was] common in the middle part of middle Dhruma', and Powers (1968) recorded it from Dhruma Unit 6 (*Tulites* Zone) and Unit 7 (*Micromphalites* Zone). Enay *et al.* (1987) renamed these units D4 and D5, and referred both to the early Bathonian. In contrast, *P. plicata* was said by Redmond (1965) to be 'common in [the] upper part of [the] basal member of [the] Upper Dhruma Formation', and was reported by Powers (1968) to occur in the 'Atash (chalky) Member, Unit 9, lower part of the Upper Dhruma. Enay *et al.* (1987) called this member 'Unit D7a', but could not determine whether it was of late Bathonian or early Callovian age. Consequently, the known stratigraphical range of this species, as here understood, is from early to late Bathonian and possibly to early Callovian also.

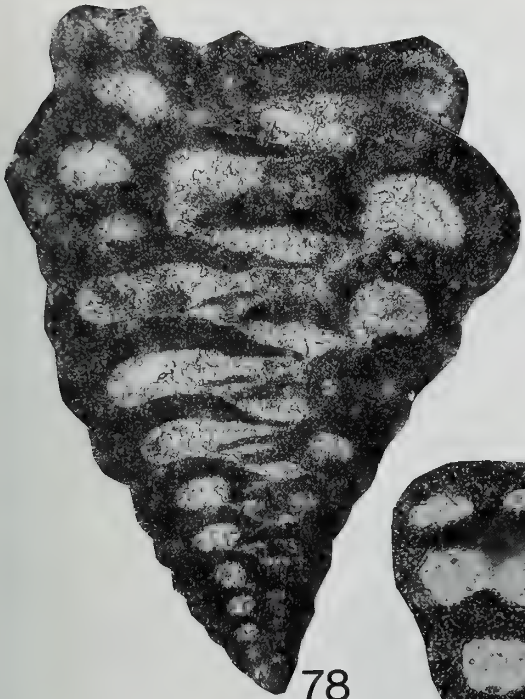
Genus ***PARAVALVULINA*** Septfontaine, 1988

TYPE SPECIES. *Paravalvulina complicata* Septfontaine, 1988.

DIAGNOSIS EMENDED. A chrysalinid with an initially quadriserial test reducing to adult triseriality; adult primary aperture interiomarginal, umbilical, covered by a broad flap which is penetrated by multiple, areal, accessory pore-like apertures; the apertural flap is convex and is attached to the top of the apertural face of the primary chamber, so that the test is terminally wholly convex; pillars link successive apertural flaps, so that the axial, umbilical part of the test is pillared, throughout its later ontogenetic stages at least; however, the primary chamber lumina, at the equatorial periphery of the test, remain unpillared; wall solid, in early ontogeny at least, sometimes becoming protocanaliculate in late growth stages.

REMARKS. Septfontaine (1988) stated that *Paravalvulina* had three chambers per whorl. However, the published photograph of the equatorial section of *P. complicata* (Septfontaine, 1981: pl. 2, fig. 15; cited under the new name by Septfontaine, 1988: 248) discloses that there can be four chambers per whorl in this species. *P. arabica* (Henson) has the same ontogenetically early quadriseriality (Figs 90, p. 144, & 95, p. 146).

DIFFERENTIATION. *Paravalvulina* is grossly homeomorphic with *Dukhania*, but differs in its quadriserial–triserial growth: megalospheric *Dukhania* is triserial to biserial in ontogeny. Also, the aperture of each chamber in the earliest whorls of *Paravalvulina* possesses a broad, imperforate lip which is depressed relative to the convexity of the true septa (similar to that of the adult, ancestral *Redmondoides*); these lips rapidly become perforated by areal, cribrate accessory apertures (like those of the nearer ancestor *Pseudomarssonella*), but the lips do not achieve a convexity equivalent to that of the true septa until the third or fourth whorl (after the proloculus) is reached. The apertural 'shields' of the adult are still less strongly convex than those of *Dukhania*, in which the terminal convexity of the *Praechrysalidina* ancestral form is displayed.



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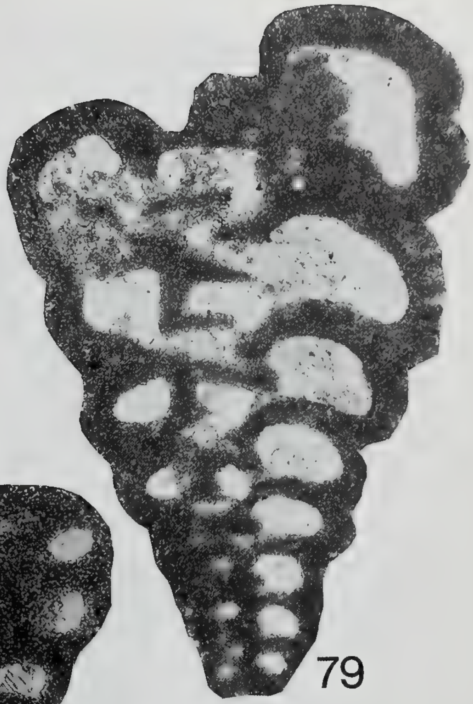

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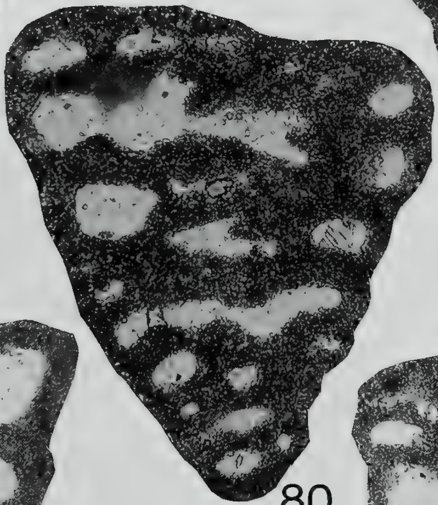

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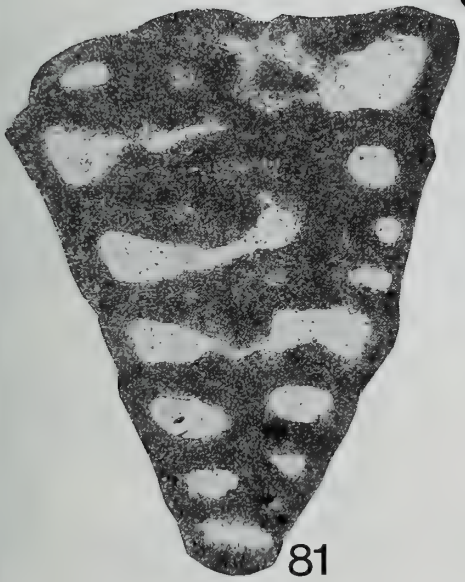

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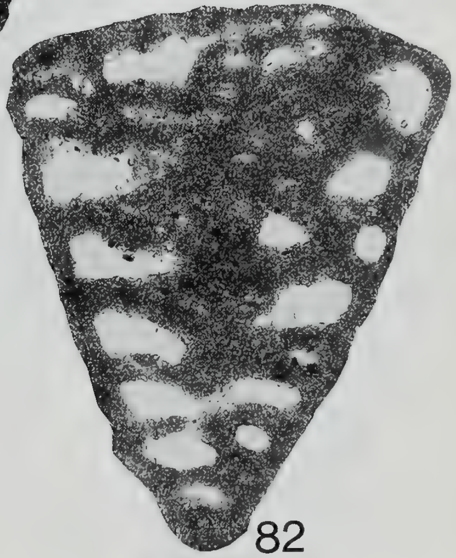

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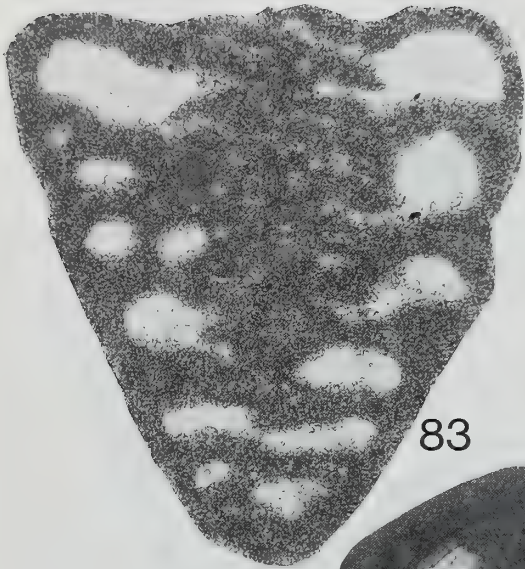
ig. 78 *Redmondoides lugeoni* (Septfontaine), BMNH P 52621, from United Arab Emirates, off-shore Abu Dhabi, Izhara Formation, probably Bajocian; length 1180 μm, × 80; note protocanaliculation and canaliculation of the walls of late chambers.

ig. 79 *Redmondoides rotundatus* (Redmond), BMNH P 52622, from off-shore Qatar, Diyab Formation, Oxfordian; length 1080 μm, × 90; note canaliculi in walls of later whorls.

ig. 80 *Redmondoides* cf. *inflatus* (Redmond), BMNH P 52623, from United Arab Emirates, off-shore Abu Dhabi, Uwainat Formation, probably Bathonian; length 520 μm, × 130.

ig. 81 *Pseudomarssonella* cf. *plicata* Redmond, BMNH P 52624, from United Arab Emirates, off-shore Abu Dhabi, Uwainat Formation, probably Bathonian; length 620 μm, × 125.

ig. 82 *Paravalvulina* sp., BMNH P 52625, from United Arab Emirates, off-shore Abu Dhabi, Uwainat Formation, probably Bathonian; length 580 μm, × 130; note the morphologically primitive development of pillars between successive apertural flaps of late ontogenetic stages.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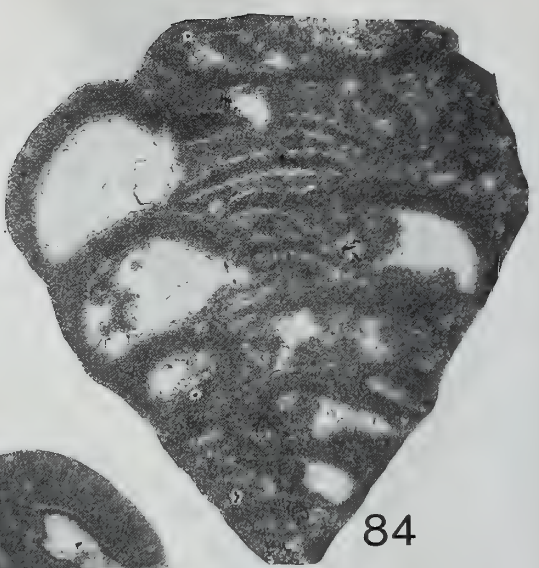
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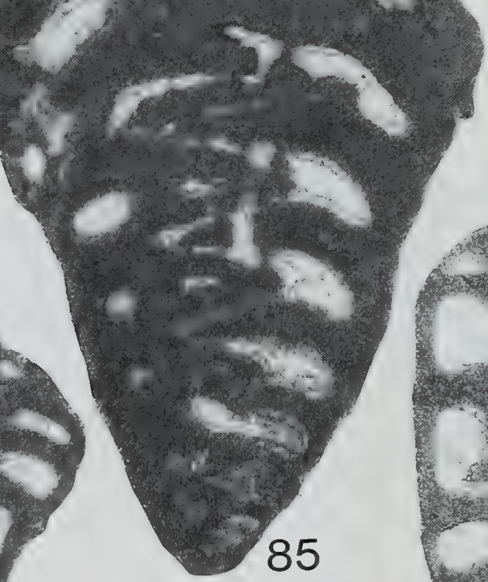
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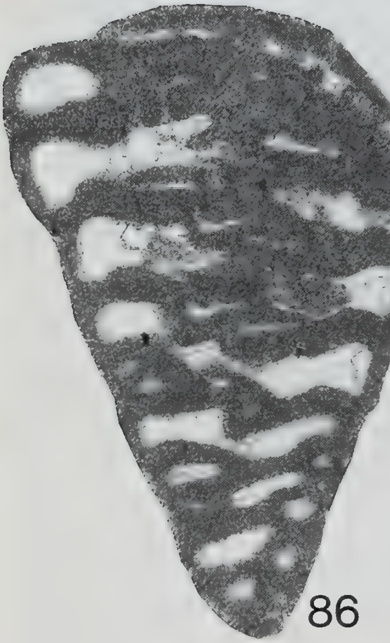
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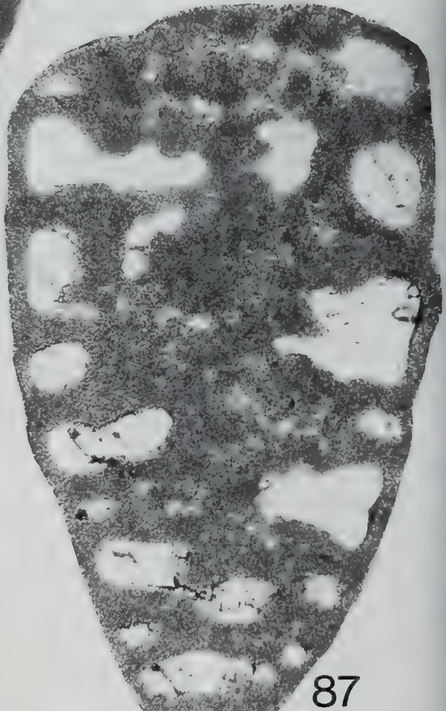
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PHYLOGENETIC AFFINITY AND SKELETAL FUNCTION. The initial quadriserial whorls, with their relatively depressed and initially imperforate. flap-like, apertural lips, indicate ancestry in species of *Redmondoides* and *Pseudomarssonella*. Canaliculaion of the walls is known in the last-formed chambers of species of both of these genera (e.g., *R. lugeoni*, *P. maxima*) and it has been reported (as a 'keriotheca') in *Paravalvulina complicata* by Septfontaine (1988). Although protocanaliculation occurs (Fig. 96, p. 146), canaliculi have not yet been observed in specimens of *P. arabica* (Henson). It seems that he development of canaliculi did not continue (or, at least, was not increased) during the course of this evolutionary lineage.

We suggest that the development of multiple, cribrate, accessory, pore-like apertures, in the closely adjacent, successive apertural 'shields', made the development of canaliculi not especially advantageous for the maintenance of adequate communication between intrathalamous cytoplasm and external sea-water; the ion-exchange function of the cytoplasm rapped in the canaliculi could have been replaced by that of he cytoplasm extruded as multiple strands through the ccessory apertural, areal pores. Only in the largest specimens, where separation of intrathalamous cytoplasm from sea-water was most complete, would the development of analiculi have been helpful.

The development of the apertural 'shields' in the umbilical rea (with intershield pillars to strengthen the structure nd to keep the successive shields spaced apart) could ave been for the partial enclosure of umbilical cytoplasm, which has been shown in many Recent rotaline foraminifera Alexander 1985) to be a reservoir of enzymes for the igestion of disaggregated nutrient particles prior to the ingestion of the nutrients, themselves, into the cytoplasm ruly inside the chambers. In such benthic rotalines (e.g. *Haynesina*, *Rosalina*) partial closure by skeletal material of he umbilical digestive cytoplasm seems to be advantageous, s it serves as a physical division between the truly intrahalamous cytoplasm, the umbilical digestive cytoplasm nd the extrusive, pseudopodial cytoplasm. It seems likely hat a similar benefit was produced by the test structure in *aravalvulina*.

The biological advantage which the umbilical structure of urassic *Paravalvulina* provided would have been repeated by he development, for the same biological reasons, of similar ructures in Cretaceous *Dukhania*. This explains the iterative volution of these gross homeomorphs.

Paravalvulina arabica (Henson, 1948) Figs 88–104

1948	*Dukhania arabica* Henson: 616; pl. 15, figs 6, 7; pl. 17, figs 1, 2.
1968	*Urgonina (Parurgonina)* (?) *arabica* (Henson); Cuvillier, Foury & Pignatti Morano: 154.
1975	*Pseudochrysalidina* (?) *arabica* (Henson); Schroeder, Geullal & Vila: 324; pl. 2, figs 1, 2.
1976	*Pseudochrysalidina arabica* (Henson); Kalantari: 36–40; pl. 6; pl. 7; pl. 8, fig. 1.

DESCRIPTION EMENDED. Test calcareous, microgranular, with rare to very rare, scattered non-calcareous grains (e.g. quartz); the microgranules of calcite in the walls are either randomly orientated or become linearly orientated, in rows perpendicular to the wall surface, to produce a protocanaliculate structure; canaliculi are not yet known. In thin section, the innermost and outermost surfaces of the walls are optically darker, and these were probably composed of granules significantly smaller, or more densely packed, than those of the main mass of the wall.

The test-form is conical, initially with a broadly acute or slightly obtuse growth angle. The test is initially quadriserial (at least in the megalospheric form) but becomes triserial in later ontogeny. Later chambers do not terminally completely cover earlier ones, but leave the terminal faces of previous chambers partly exposed. The primary aperture of each chamber in the nepionic to ephebic stages is simple, umbilical and interiomarginal, covered by a broad, flap-like lip; in neanic–ephebic growth the flap becomes penetrated by multiple, areal, cribrate, accessory apertural pores; the opening of the primary aperture becomes higher and the flap becomes attached to the highest part of the primary apertural face; the flap becomes a trematophore-like perforate 'shield' (as named by Henson, 1948). All the shields of the last-formed chambers (distinct from the convex terminal faces of the last-formed chambers themselves, which remain exposed) span much or all of the umbilicus and create a slightly, but distinctly, convex termination to the test.

Internally, many pillars are developed, even in the nepionic stage, from the interpore areas of the shields, to reach and fuse with the shields of immediately preceding chambers. The lumina of the chambers themselves, marginal to the shields, lack pillars. In neanic–ephebic growth, the pillars multiply, often crowding together, producing a densely pillared ('labyrinthic') umbilical zone, central to the long axis of the test.

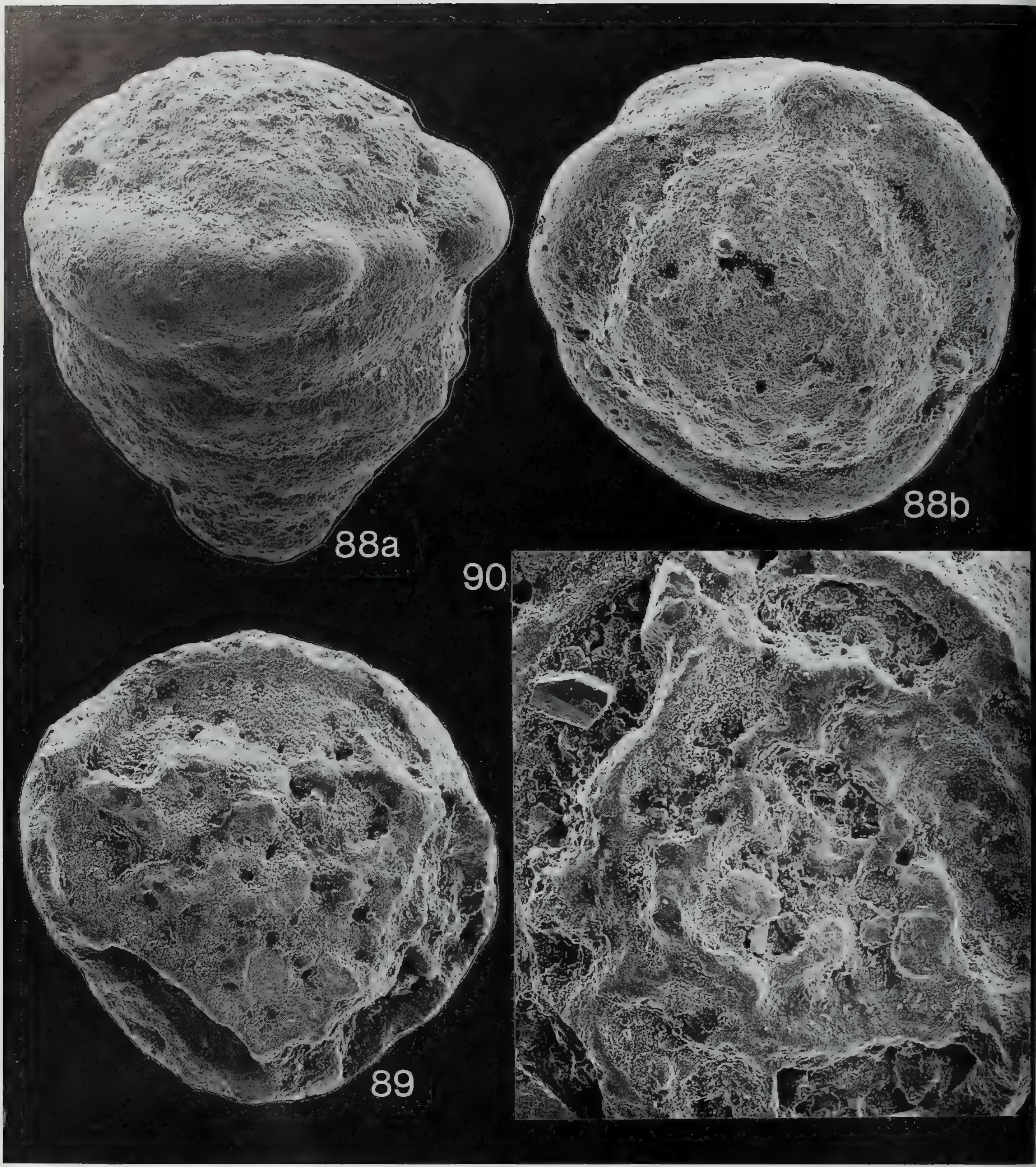
g. **83** *Pseudomarssonella* cf. *maxima* Redmond, BMNH P 52626, from United Arab Emirates, off-shore Abu Dhabi, Lower Araej Formation, Bajocian or Bathonian; length 600 µm, × 130.

g. **84** *Pseudomarssonella* cf. *bipartita* Redmond, BMNH P 52627, from off-shore Qatar, Uwainat Formation, probably Bathonian; length 1030 µm, × 75.

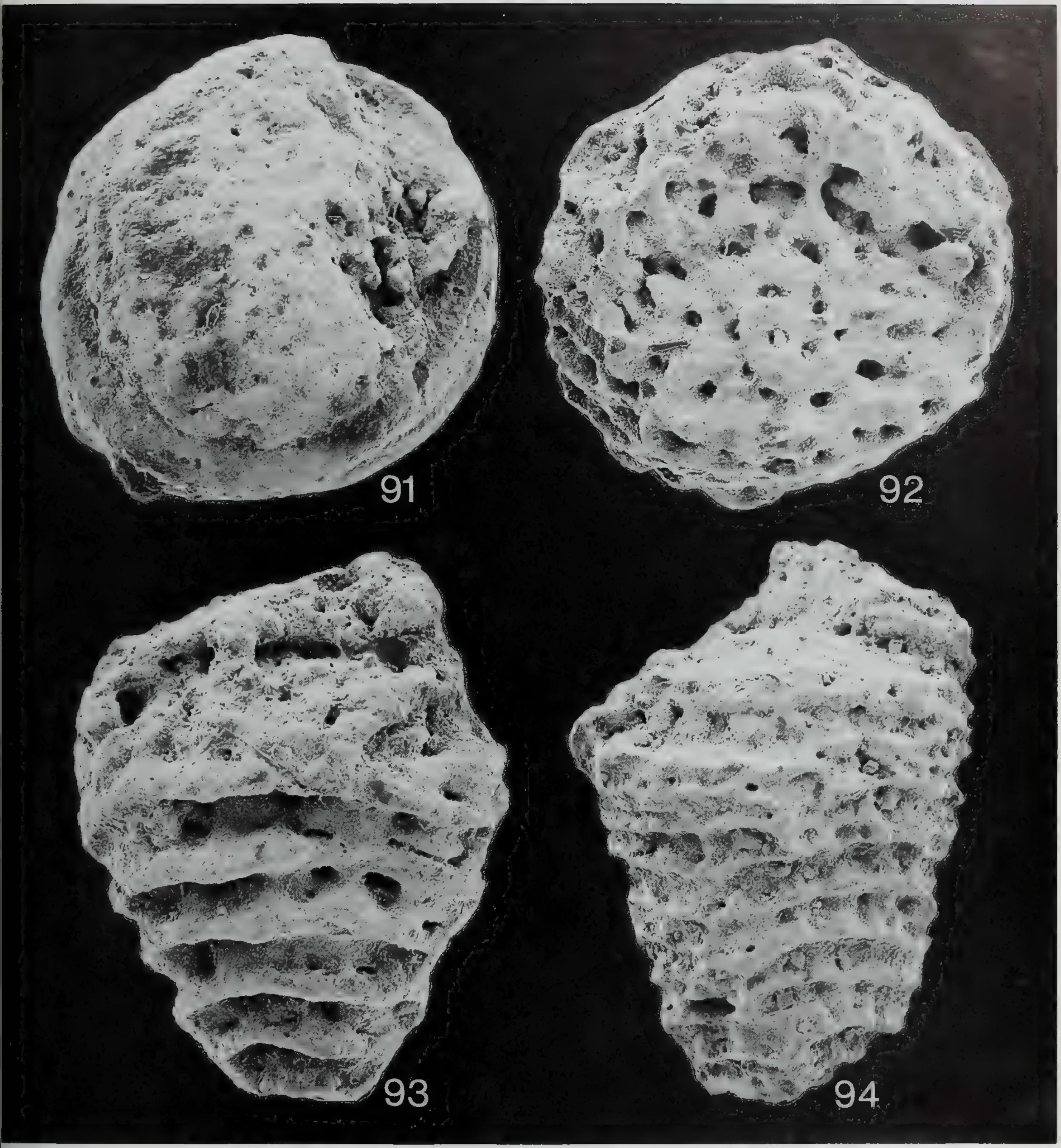
g. **85** '*Praechrysalidina*' cf. *infracretacea* Luperto Sinni, BMNH P 52628, from United Arab Emirates, subsurface on-shore Abu Dhabi, Mauddud Formation (late Albian–mid Cenomanian); axial section, length 1540 µm, × 65; incomplete pillars between the cribrate, apertural flaps of late whorls herald the evolution of the continuously, completely pillared *Dukhania* (compare Figs 17–19 & 21–26, p. 112–114), and mimic the development of incomplete pillars in the late ontogeny of '*Pseudomarssonella*' in its evolution to *Paravalvulina* (see Fig. 86).

g. **86** '*Pseudomarssonella*' cf. *plicata* Redmond (compare Figs 75–77, p. 139), BMNH P 52629, from United Arab Emirates, off-shore Abu Dhabi, Lower Araej Formation, Bajocian or Bathonian; with incomplete pillars between the apertural flaps of the last whorl in the evolution of *Paravalvulina*.

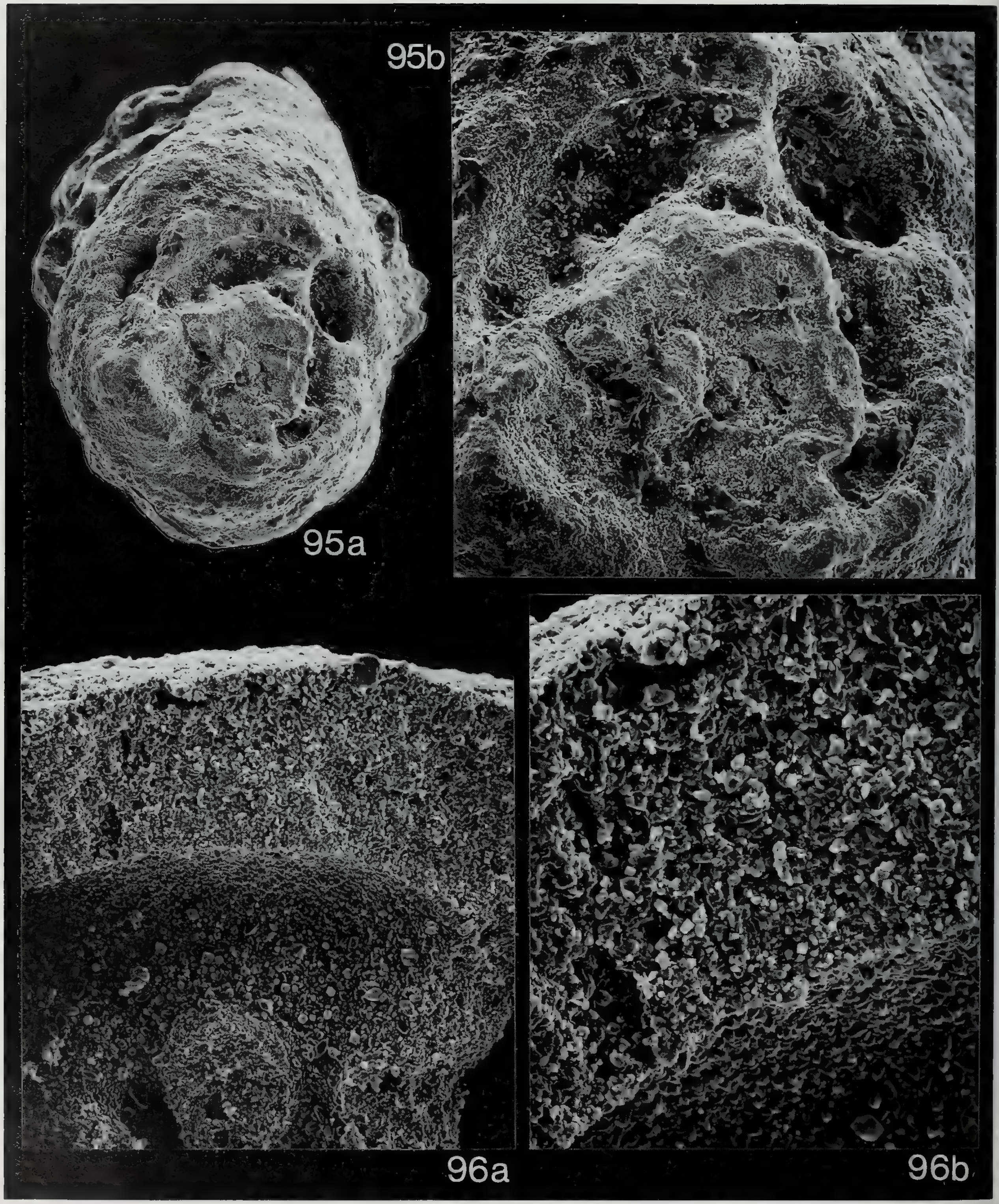
g. **87** '*Paravalvulina*' aff. *complicata* Septfontaine, BMNH P 52630, from United Arab Emirates, off-shore Abu Dhabi, Upper Araej Formation, probably Callovian; length 780 µm, × 125; a few incomplete, and rarer complete, pillars are developed between the apertural flaps.



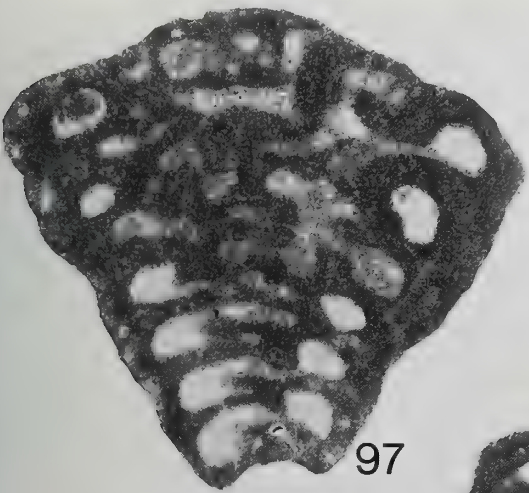
Figs 88–90 *Paravalvulina arabica* (Henson), strictly topotypic paratypes, from Qatar, Well Dukhan-2, 4375–4380 ft depth, Hauterivian. Fig 88a–b, BMNH P 52631, entire specimen; a, axial view (length 1,240 μm), × 70; b, terminal view, × 70. Fig. 89, BMNH P 52632; equatori view of specimen from which the initial end has been broken, showing initial quadriseriality and umbilical pillars between the cribrate, pore like apertures of the umbilical, apertural flaps; breadth 1,100 μm, × 70. Fig. 90, BMNH P 52633; initial end of specimen which has lost i chamber walls, showing initial quadriseriality, × 110.



gs 91–94 *Paravalvulina arabica* (Henson); specimens which have lost part or all of their outer chamber walls; from Qatar, Well Dukhan-2, 4375–4380 ft depth, Hauterivian. Fig. 91, BMNH P 52634, terminal view (breadth 1,620 µm), × 50, with umbilical-apertural flap partly broken, showing internal, umbilical pillars. Fig. 92, BMNH P 52635, oblique-axial view (breadth 1,080 µm), × 70, showing umbilical pillars between the cribrate apertural pores in the umbilical-apertural flaps. Fig. 93, BMNH P 52636, axial view (length 1,100 µm), × 80; showing main chambers free of pillars (which fill the inner, umbilical area). Fig. 94, BMNH P 52637, axial view (length 1,580 µm), × 60, of specimen from which the chambers, themselves, have been eroded, leaving only the intensely pillared umbilical regions of successive whorls.



Figs 95–96 *Paravalvulina arabica* (Henson), from Qatar, Well Dukhan-2, 4375–4380 ft depth, Hauterivian. Figs 95a–b, BMNH P 52638; initial view, showing initial quadriseriality; a (breadth 1,200 µm), × 70; b, enlargement of initial whorls, × 150. Figs 96a–b, BMNH P 52639; microgranular, calc-agglutinated wall, broken in cross-section, displaying the shape, size and distribution of the constituent calcareous microgranules; a, broken wall, adjacent interior surface, broken pillar and adjacent pore, × 350; b, enlargement of wall structure, × 800, showing partial linear arrangement of columns of calcareous microgranules (partial protocanaliculation).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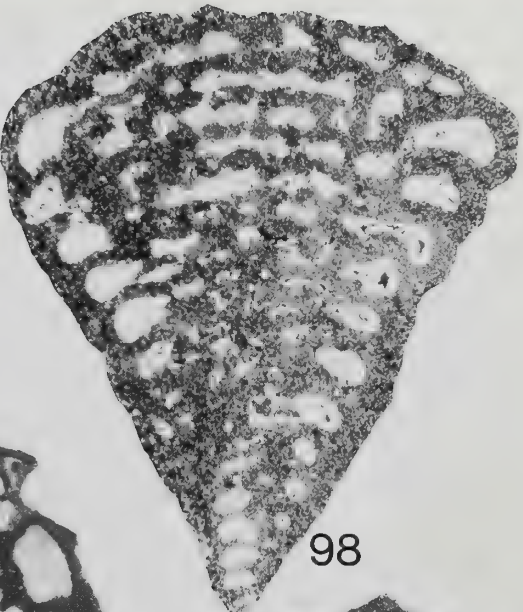
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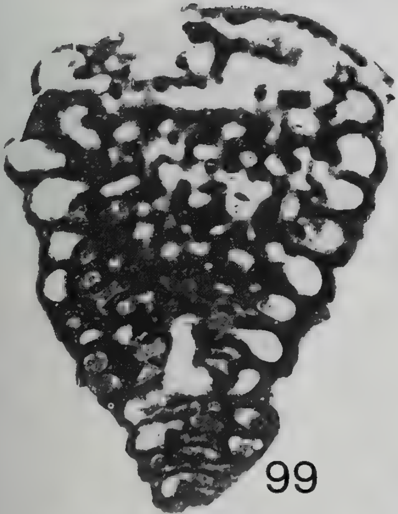
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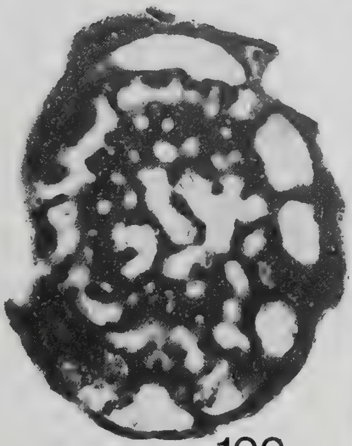
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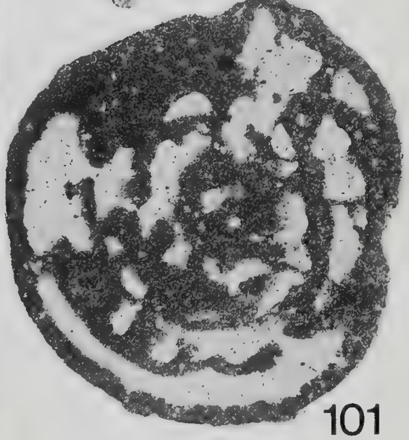
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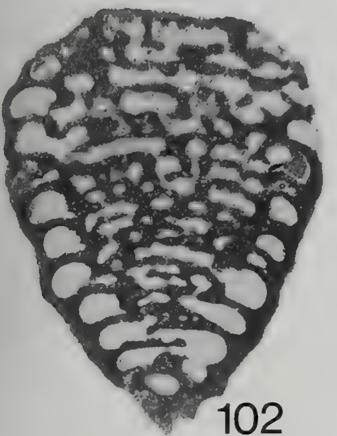
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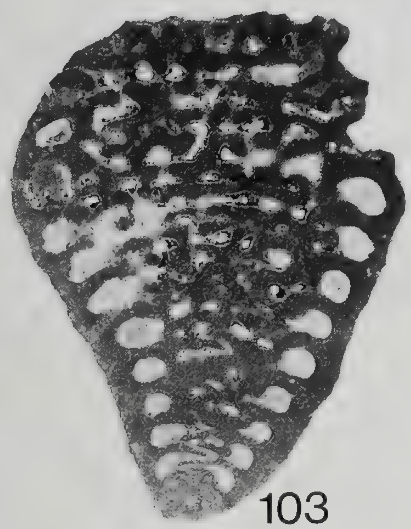
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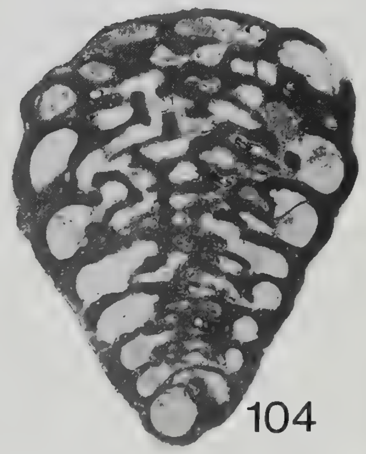
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Figs 97–104 *Paravalvulina arabica* (Henson). Fig. 97, BMNH P 52640, from Qatar, Well Dukhan-3, 5117–5137 ft depth, Hauterivian; axial section length 820 µm, × 80. Fig. 98, BMNH P 52641, from United Arab Emirates, Well Jumayla-1 (Jamayla-1), 10,041.08 ft depth, Zakum Formation, Valanginian; axial section (length 1,740 µm), × 50. Figs 99–100, paratypes, from Qatar, Well Dukhan-2, 4375–4380 ft depth, originally dated as 'Infravalanginian' but now referred to the Hauterivian. Fig. 99, BMNH P 39108, axial section (length 2240 µm), × 30. Fig. 100, BMNH P 39107, equatorial section (maximum breadth 1780 µm), × 35. Figs 101–104, strict topotypes (locality and depth as for P 39107–8). Fig. 101, BMNH P 52642, equatorial section (maximum breadth 1400 µm), × 40. Fig. 102, BMNH P 52643, axial section (length 1920 µm), × 30. Fig. 103, BMNH P 52644, axial section (length 1960 µm), × 35. Fig. 104, BMNH P 52645, axial section (length 1800 µm), × 35.

DIFFERENTIATION. *Paravalvulina arabica* differs from *P. complicata* Septfontaine in possessing much narrower true chamber lumina and a broader and more densely pillared umbilical zone. The true septa of *P. arabica* are much thinner relative to chamber height, being about 20% of the total chamber height, compared to 35–40% in *P. complicata*.

REMARKS. Although Henson (1948) referred this species to his new genus *Dukhania* without expressing doubts, the specimens which were labelled in the Henson and associates collection (and which are now in the Natural History Museum, London) were only doubtfully assigned to *Dukhania* (i.e., being labelled '*Dukhania*? *arabica* Henson MS'). This doubt is now explained by the present study and by the revised assignment of the species to the genus *Paravalvulina* Septfontaine. *P. arabica* (Henson) and *Dukhania conica* Henson (p. 111) are phylogenetically distinct, gross homeomorphs.

Cuvillier *et al.* (1968) noted that there were resemblances between *Dukhania arabica* Henson and the newly proposed type species of their new subgenus, *Urgonina (Parurgonina) caelinensis*, so much so that they hesitantly referred Henson's species to that subgenus. However, the adult *Parurgonina* is uniserial, and has been considered by Septfontaine (1988) to be an independent, Oxfordian–'Portlandian' descendant from '*Valvulina lugeoni*' (i.e., from *Redmondoides* sp.). Schroeder *et al.* (1975) photographed axial sections of two topotypes of *Dukhania arabica* (from well Dukhan-2, Qatar, 4375–4380 ft depth), and these, with sections of two other topotypes, failed to show the canaliculate ('keriothecal') walls believed to characterize *Parurgonina caelinensis* (as photographed by Schroeder *et al.*, 1975: pl. 1, fig. 3 and pl. 2, figs 3–5). Nevertheless, protocanaliculation can occur weakly in the walls of *Paravalvulina arabica* (Figs 96–98) and a distinction based solely on such a character must not be expected to be reliable.

STRATIGRAPHY. *P. arabica* was originally obtained by Henson (1948) from limestones and marls (also containing *Pseudocyclammina lituus* (Yokoyama) as described by Banner & Whittaker, 1991) drilled in Qatar (the holotype and paratypes from well Dukhan-2, at 4375–4380 ft depth; other specimens coming from well Dukhan-3, at 5117–5137 ft depth). These beds were once thought to be of 'Infravalanginian' age but are now referred to the Hauterivian (Banner & Whittaker 1991). *Paravalvulina arabica* was also found (and well illustrated) by Kalantari (1976) in the Valanginian–Hauterivian Fahliyan Formation of south-west Iran. These are the youngest known occurrences of *Paravalvulina*. Septfontaine (1988) considered the range of the genus to be that known only for the type species, i.e. 'U. Bajocian (?) to Bathonian', as the type specimens of *P. complicata* were obtained by him from Bathonian limestones of Sardinia. We have found morphologically primitive specimens of *Paravalvulina* sp. in the Uweinat Formation (probably Bathonian), drilled off-shore at Abu Dhabi (Fig. 82, p. 141), and other specimens, here called *'P.'* aff. *complicata*, with more complete inter-flap pillars (Fig. 87), from the Upper Araej Formation (probably Callovian) of the same area. The known and proved biostratigraphic range of the genus is Bathonian to Hauterivian.

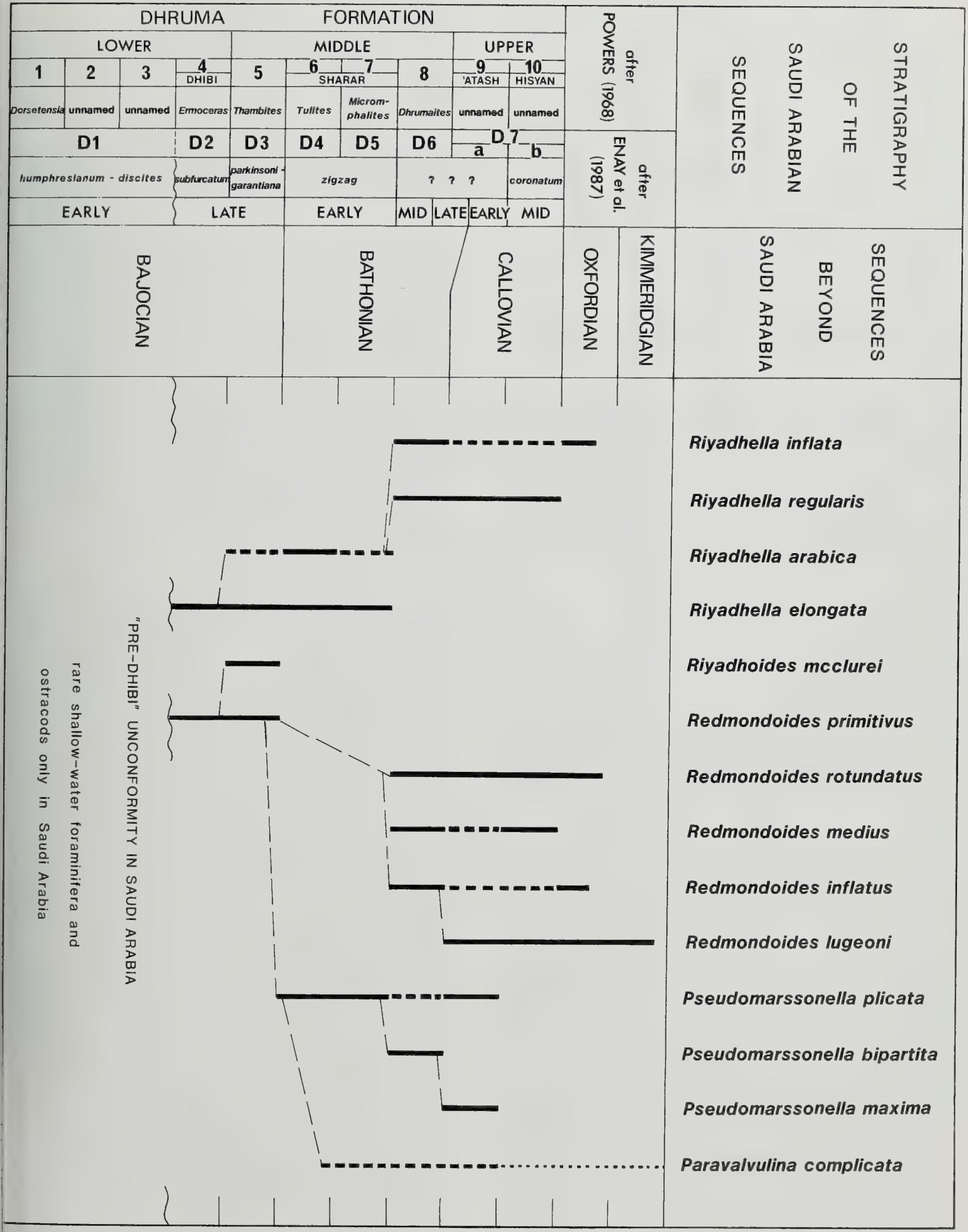
CONCLUSIONS

The family Chrysalidinidae contains taxa which are calc-agglutinating, and in which the calcareous microgranules may align so that their walls become protocanaliculate. True canaliculi develop in the walls of individuals of many taxa, but at differing stages of growth. No stratigraphically significant, phylogenetic sequence of development from randomly to protocanaliculately orientated microgranules, or from protocanaliculate to canaliculate wall structure, can be perceived in the Chrysalidinidae. Consequently, it is believed that chrysalidine taxa, at specific or higher categories, cannot be distinguished on these criteria. This conclusion differs from that which may be applicable to other family-groups (e.g., the Eggerellidae, Textulariidae, Valvulinidae, Verneuilinidae, etc.), but it exemplifies the rule that morphological characters have differing degrees of taxonomic importance in different supraspecific taxa. For example, the presence or absence of costae may not even distinguish species in many genera of the Nodosariacea, but they would characterize species in the Heterohelicacea and genera in the Globotruncanacea. The Foraminiferida are too diverse to be governed by simple rules of universal, unchangeable regulation.

Like all other foraminiferid skeletal structures, the wall-structures of the Chrysalidinidae almost certainly had a biological function; it is possible (even probable) that canaliculi had the same function as that possessed by the narrow hypodermal alveoli of some Cyclamminidae (Loftusiacea), and allowed ionic exchange between intrathalamous cytoplasm and external sea-water. In the Chrysalidinidae, this may have become advantageous in different stages of ephebic growth under different environmental conditions, and was not developed if it was not useful. It certainly does not apppear to have been a standard development, as it was in other foraminiferid families.

The Chrysalidinidae are morphologically and phylogenetically divisible into the neanically quadriserial, almost wholly Jurassic Paravalvulininae, and the neanically triserial, Cretaceous Chrysalidininae. These two subfamilies are believed to have had different evolutionary origins, and different detailed patterns of evolution, but both were Tethyan, both were calc-agglutinating with similar histories of canaliculation, and both evolved pillared forms which were closely homeomorphic (*Paravalvulina* and *Dukhania*). In any system of classification, it would seem sensible, practicable and useful to keep these particular genera distinct but close together.

Even with an amalgamation of the Redmond Arabian collection, the Henson and associates collection from Iraq. Iran and Qatar, and additional material from the United Arab Emirates, Oman and elsewhere, we still do not know the ancestor of the earliest known Paravalvulininae. The oldest known genera (*Riyadhella* and *Redmondoides*) both appear in the Late Bajocian (Fig. 105). Species of the former occur in beds at least as young as Oxfordian, while species of the latter are known from beds as young as Kimmeridgian. Stratigraphically late species, at least, of both genera (*Riyadhella inflata*, *Redmondoides inflatus*) spread into more northerly areas, while at least one of the latter (*Redmondoides lugeoni*) became widespread throughout Tethys. Another, stratigraphically early and morphologically simple, genus (*Riyadhoides*) was short-lived (Bajocian) and apparently confined to central Tethys. The development of cribrate apertures in non-pillared forms (species of *Pseudomarssonella*) appears to have been confined to the Bathonian and Callovian, but umbilical pillaring developed rapidly – it is recorded (as *Paravalvulina*, by Septfontaine, 1988) also from the Bathonian of Tethys. The evolution of pillared forms



ig. 105 Stratigraphical ranges of the Jurassic Paravalvulininae. Continuous lines represent firmly known occurrences, dashed lines represent doubtfully dated occurrences or stratigraphically intermediate intervals, while the dotted line (*Paravalvulina complicata*) links to the early Cretaceous occurrence of the last member of this subfamily, *P. arabica*.

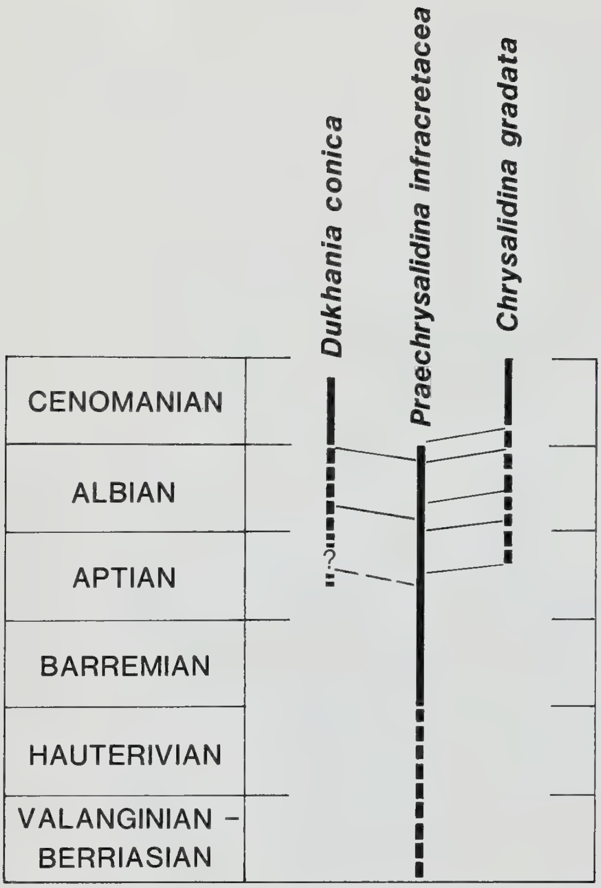


Fig. 106 Stratigraphical ranges of the early to mid-Cretaceous taxa of the Chrysalidininae; dashed lines represent the occurrences of ancestral, morphologically primitive forms, while continuous lines represent the occurrence of typical forms of the named species.

seems to have been gradual, as morphologically simple forms (e.g., Figs 85, 86, p. 142) are known from beds probably as young as Callovian. *Paravalvulina arabica*, also from Tethys, occurred in the earliest Cretaceous, and was the last of the Paravalvulininae.

The Chrysalidininae (Fig. 106) seem to have evolved independently and directly from *Verneuilinoides* in the earliest Cretaceous, by the appearance of the unpillared *Praechrysalidina*. The development of pillars (in the late Aptian–Albian) was gradual, producing gross homeomorphs of the antecedents of true *Paravalvulina* (e.g., Fig. 85; compare Figs 86 and 87), and completely pillared forms were clearly developed in the Cenomanian. These included the rapidly tapering, terminally biserial *Dukhania* and the slowly tapering, terminally triserial *Chrysalidina*. Although both were of Cenomanian age, they appear to have developed independently from *Praechrysalidina*: the former seems to have been confined to central Tethys, and to have had no descendants, while the latter spread throughout western and central Tethys (at least from western France to Yemen and Oman) and probably gave rise to *Accordiella* in the Coniacian–Campanian.

The reillustration of all the above-mentioned taxa (except *Accordiella*), whenever possible both by the SEM of solid specimens and by the optical photography of their thin sections, has made possible their umambiguous reidentification, and, consequently, their limited stratigraphical ranges have proved their potential use in the biostratigraphy of the mid Jurassic – late Cretaceous neritic marine sediments of, at least, central and western Tethys.

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Bryozoans from the Llanbedrog Mudstones (Caradoc), north Wales.

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SYNOPSIS. A diverse bryozoan fauna is described from the Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, north Wales. The fauna is dominated by trepostomes (nine species), although one cystoporate and one cyclostome species are present. Three new trepostome species, *Stigmatella oakleyi*, *Pedrogopora taylori*, and *Diplotrypa nontabulata* are described; *Pedrogopora* is a new genus.

A lectotype for *Prasopora grayae* Nicholson & Etheridge 1877 is selected.

INTRODUCTION

Bryozoans are one of the major components of Ordovician faunas. Whilst they are well known from North America and the Soviet Union, their study has been largely neglected in Britain. This neglect may be partly attributed to poor preservation and the time taken to prepare specimens, and partly to the lack of any strong tradition of bryozoan research in Britain. Bryozoan specimens from the Ordovician of Britain are commonly present in museum collections (e.g. Natural History Museum, Sedgwick Museum and British Geological Survey), but they are usually decalcified moulds. This makes hem difficult to identify even to family level. Calcified pecimens frequently go unnoticed in the field except where a arge proportion of the rock consists of bryozoans.

MATERIAL

The Llanbedrog Mudstones (Soudleyan, Caradoc) crop out on the western side of the A449 road south of Llanbedrog, Gwynedd, north Wales (National Grid Reference SH 322314). Fossils are unevenly distributed throughout the rock, a calcareous mudstone. Bands of decalcified bryozoans can be identified on the surface of the outcrop. When these regions were excavated calcified colonies were revealed. Brachiopods (e.g. *Leptaena* sp.) and trilobites (e.g. *Calymene* sp. and *Illaenus* sp.) were also found at this locality.

Matley (1938) described the geology of the area around Pwllheli, Llanbedrog and Madryn. This includes a description and faunal list of the Llanbedrog Mudstones. Recorded on the list are ‘cf. *Monticulipora lens* auct., *Ptilodyctya*? and indeterminate polyzoa’; no illustrations are included.

The material examined here comprises specimens collected recently in the field, and a Natural History Museum collection from the same locality made by the late Dr K. P. Oakley. The Oakley collection includes thin sections prepared from over thirty specimens.

The bryozoan fauna is diverse, consisting of 11 species, three of which are new. Trepostomes dominate with nine species, but one cystoporate and one cyclostome species are also present. The cyclostome species is very small and quite abundant but has only been recognized in randomly orientated peels. Only a brief description of this species is included herein (p. 167) because it has recently been described in full elsewhere (Buttler 1989).

Table 1 Summary of the biometric details of all trepostome species from the Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. In each case, upper left figure is the mean, followed by the number of specimens in brackets. Lower figures are the range. All measurements are in millimetres except for ZMM, CMM, AZ and AMM (*). ZOW = zoarial diameter, EXW = exozonal width, MXZD = maximum autozooecial diameter, MNZD = minimum autozooecial diameter, MXMD = maximum mesozooecial diameter, ZWT = autozooecial wall thickness, ZMM = autozooecia per mm, DEX = distance between exozonal autozooecial diaphragms, DEN = distance between endozonal autozooecial diaphragms, DMEX = distance between exozonal mesozooecial diaphragms, DMEN = distance between endozonal mesozooecial diaphragms, CMM = number of cystiphragms per mm, AD = acanthostyle diameter, AZ = number of acanthostyles per autozooecium, AMM = acanthostyles per square mm.

Species	ZOW	EXW	MXZD	MNZD	MXMD	ZWT	ZMM *	DEX	DEN	DMEX	DMEN	CMM *	AD	AZ *	AMM *
Stigmatella oakleyi	8·26 (9) 4·0–15·0	1·79 (34) 1·14–2·85	0·29 (36) 0·17–0·48	0·2 (36) 0·11–0·32	0·12 (36) 0·04–0·23	0·06 (34) 0·02–0·11	9·12 (36) 5·5–13	0·15 (36) 0·06–0·36	0·31 (1) 0·25–0·4	0·1 (36) 0·04–0·21	–	–	0·04 (34) 0·02–0·08	2·86 (34) 1–6	21 (28) 8–34
Pedrogopora taylori	5·57 (7) 4·0–8·0	1·67 (4) 1·24–2·28	0·36 (6) 0·23–0·51	0·24 (6) 0·15–0·4	0·14 (6) 0·04–0·29	0·14 (6) 0·08–0·23	4·73 (6) 4–5·5	0·19 (1) 0·19	–	0·09 (7) 0·04–0·21	–	–	0·06 (5) 0·04–0·09	6·73 (3) 5–9	8·67 (2) 7–10
Diplotrypa pseudopetropolitana	–	–	0·44 (1) 0·42–0·46	0·35 (1) 0·32–0·4	0·16 (1) 0·1–0·23	–	4·75 (1) 4·5–5	–	0·53 (1) 0·38–0·68	–	0·07 (1) 0·04–0·1	–	–	–	–
Diplotrypa nontabulata	9·5 (2) 9·0–10·0	–	0·44 (4) 0·3–0·57	0·38 (4) 0·27–0·48	0·23 (4) 0·08–0·44	–	–	5·83 (4) 4·5–7·0	–	0·15 (3) 0·1–0·3	0·16 (3) 0·08–0·23	–	–	–	–
Hallopora cf. *tolli*	5·0 (1) 5·0	0·86 (1) 0·86	0·31 (1) 0·27–0·34	0·23 (1) 0·17–0·32	0·13 (1) 0·08–0·19	0·08 (1) 0·06–0·1	6·83 (1) 6·5–7	0·11 (1) 0·08–0·17	0·21 (1) 0·17–0·25	0·05 (1) 0·04–0·06	0·07 (1) 0·06–0·1	–	–	–	–
Eridotrypa cf. *kilbartiensis*	2·5 (1) 2·5	0·76 (1) 0·76	0·12 (1) 0·11–0·13	0·1 (1) 0·1–0·11	–	–	–	0·11 (1) 0·08–0·13	–	–	–	–	–	–	–
Prasopora grayae	11·0 (2) 10·0–12·0	–	0·41 (2) 0·34–0·51	0·31 (2) 0·29–0·36	0·13 (1) 0·08–0·17	–	6·67 (2) 5–9	0·12 (1) 0·08–0·23	0·1 (2) 0·04–0·13	–	0·06 (1) 0·04–0·1	8·91 (2) 7–11	–	–	–
Prasopora thorali	30 (1) 30	–	0·43 (2) 0·29–0·55	0·35 (1) 0·27–0·48	0·14 (2) 0·08–0·23	0·029 (2) 0·02–0·06	5·55 (2) 3–8	0·14 (2) 0·06–0·23	0·17 (2) 0·1–0·29	–	0·1 (2) 0·08–0·13	6·21 (2) 5–8	–	–	–
Mesotrypa sp.	8·0 (1) 8·0	–	0·34 (1) 0·27–0·42	–	0·17 (1) 0·13–0·19	–	–	–	–	0·11 (1) 0·1–0·13	0·12 (1) 0·06–0·19	–	0·04 (1) 0·04–0·05	–	–

A total of nine genera have been described from the Caradoc Llanbedrog Mudstones. Only one of these, *Pedrogopora* gen. nov. (p. 157), is endemic to north Wales; all the rest are cosmopolitan, known from North America and Baltoscandia. A wide generic dispersal may have been caused by a long-lived planktotrophic larval phase which encouraged dispersal. Taylor & Cope (1987) consider that early stenolaemates may have inherited this phase from their ctenostome ancestors.

Four of the total 11 species have not been previously described outside north Wales. Three of these species are new and one has been left in open nomenclature. It is impossible to tell if this apparent endemism reflects the true condition, or is the result of selective preservation and/or sampling.

Three species, *Hallopora* cf. *tolli*, *Ceramoporella distincta* and *Kukersella borealis* have very broad biogeographical ranges. They are known from both North America and Baltoscandia. The majority of the British Isles was separated, during the Lower Ordovician, from North America (Laurentia) by the Proto-Atlantic Iapetus Ocean. Pickering *et al.* (1988), using a variety of palaeontological, stratigraphical, structural, geophysical and igneous evidence considered that by the end of the Ordovician the Iapetus Ocean was partially closed, with only narrow marine seaways persisting to the Middle Silurian. During the Caradoc the Iapetus did not form an impenetrable barrier to bryozoan dispersal. *Prasopora grayae* is also known from both sides of the Iapetus, because Scotland was located on the Laurentian margin.

SYSTEMATIC PALAEONTOLOGY

The terminology in all descriptions is that of Boardman *et al.* (1983). Trepostomata genera are placed in families based on Astrova (1978) and Cystoporata genera on Utgaard (*in* Boardman *et al.* 1983). Family level classification is generally unsatisfactory in Palaeozoic trepostomes and is currently being revised for the Treatise on Invertebrate Paleontology by R. S. Boardman.

Three taxa could not be conclusively identified to specific level. In these cases the species are referred to as 'cf.' and 'sp.', based on the recommendations of Bengston (1988).

Biometric details for all trepostome species are tabulated (Table 1). Each measurement was made up to seven times per specimen. The mean and range are calculated for each parameter. Raw data can be found in the author's unpublished Ph.D. thesis (Buttler 1988). All specimens are thin sections or acetate peels.

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order **TREPOSTOMATA** Ulrich, 1882
Suborder **HALLOPOROIDEA** Astrova, 1965
Family **HETEROTRYPIDAE** Ulrich, 1890

Genus ***STIGMATELLA*** Ulrich & Bassler, 1904

Stigmatella oakleyi sp. nov. Figs 1–4, 8

HOLOTYPE. BMNH PD 2641; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

PARATYPES. BMNH PD 2639, 2655, 2658, 2664, 2664a, b, 2665–74, 2685–6, 2688, 2692–3, 2695, 2701, 2716, 2718, 8283–96; all from the same horizon and locality as the holotype.

NAME. For the late Dr K. P. Oakley, formerly of the Natural History Museum, who first collected and sectioned trepostome bryozoans from the Llanbedrog Mudstones.

DIAGNOSIS. Colony large, ramose. Autozooecia have very thin, wavy walls in endozone, are parallel to branch axis, and then curve out abruptly to zoarial surface. Zooecial walls thicken irregularly in exozone. Autozooecia polygonal in transverse section, rounded to petaloid in shallow tangential section. Polygonal-rounded mesozooecia common, originating in the outer endozone and inner exozone. Diaphragms present in exozonal autozooecia, common in mesozooecia. Acanthostyles abundant in exozone.

DESCRIPTION. Zoaria erect with cylindrical branches, on average 8·26 mm in diameter. The surfaces of all specimens are abraded. Autozooecia meander but generally are parallel to the branch axis at the centre of the colony. They curve outwards abruptly in the outer endozone and meet the zoarial surface at 90°. Autozooecia within the endozone have very thin walls.

The exozone is usually thick, with an average diameter of 1·79 mm. It is recognized by simultaneous irregular thickening of the zooecial walls and a change in zooecial orientation. Transverse sections of autozooecia are polygonal in the endozone, becoming rounded to petaloid in the exozone, as seen in shallow tangential sections. Autozooecial diameters average 0·20 mm × 0·29 mm in the exozone. Orally-deflected basal diaphragms are rare to absent in the endozone but present within the autozooecia in the exozone, where they are spaced on average 0·15 mm apart.

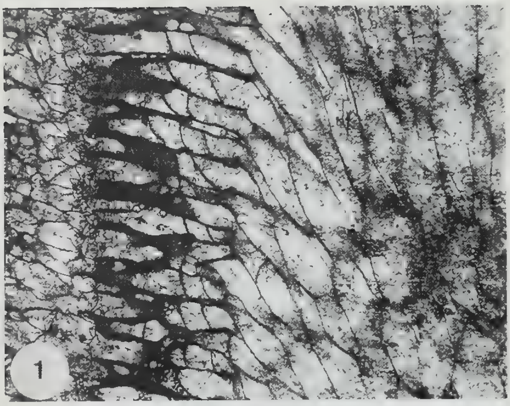
Mesozoecia are common and originate in the outer endozone and exozone. They are polygonal-rounded in shallow tangential sections and have a maximum diameter which averages 0·12 mm. Orally-deflected basal diaphragms are common in the mesozooecia, spaced on average 0·1 mm apart. In the outer endozone/inner exozone the mesozooecia are thinner and constricted at the positions of the diaphragms, producing a beaded appearance.

Acanthostyles are short and abundant, with an average diameter of 0·04 mm and density of 21 per mm^2. They originate throughout the exozone and frequently indent the zooecial apertures, producing a pronounced petaloid shape. A hyaline core is surrounded by steeply dipping conical laminae.

Autozooecial wall thickness averages 0·06 mm in the exozone. Wall microstructure is composed of inclined U-shaped laminae. Zooecial wall boundaries consist of wide regions of granular calcite. The microstructure is frequently disrupted by large acanthostyles. Some zooecia, especially mesozooecia, are infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

It is common to find hollow 'cyst-like' structures within autozooecia in some zoaria (Figs 4b, c). These are spherical, average 0·05 mm in diameter, and occur singly or in groups. They are attached to the sides of the zooecial walls or to the centre of diaphragms, and their laminae are continuous with zooecial linings.

Maculae, consisting predominantly of mesozooecia, have been observed in shallow tangential section (Fig. 3). Large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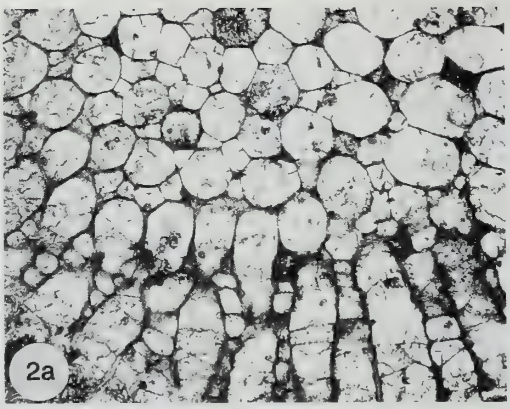
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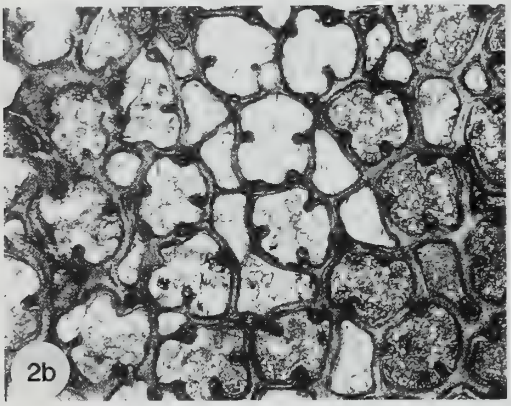
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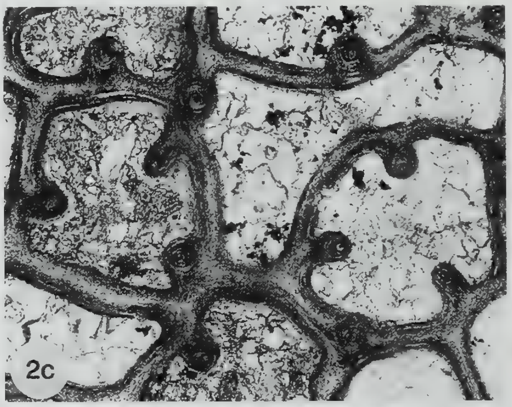
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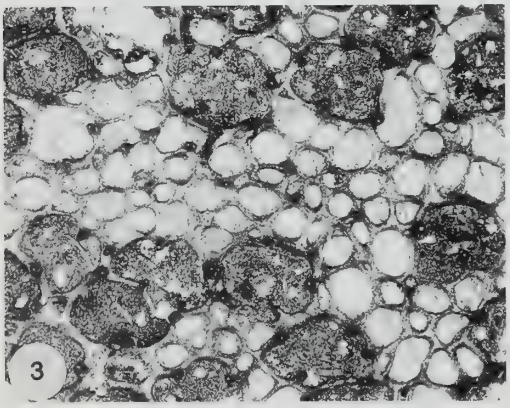
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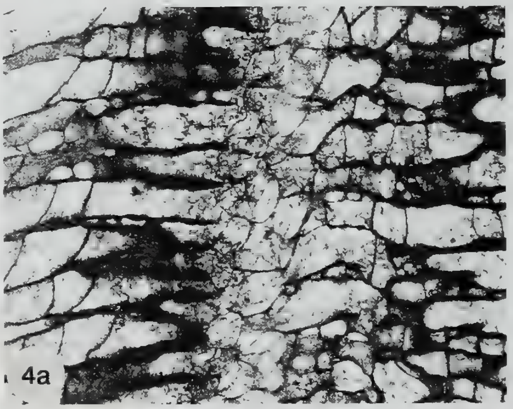
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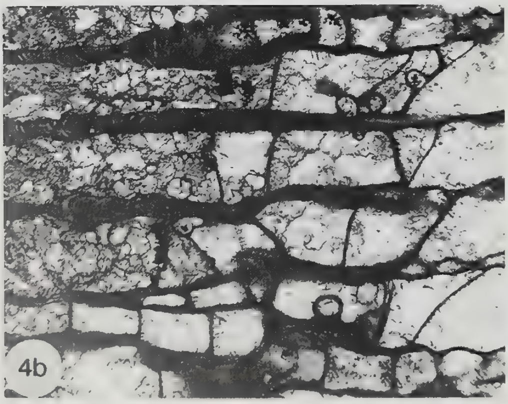
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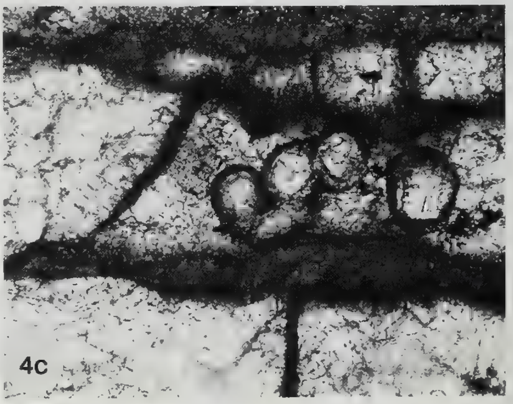

4c

intraspecific overgrowths are common and are composed of exozonal and outer endozonal elements.

REMARKS. *Stigmatella oakleyi* sp. nov. is primarily characterized by the erect colony form and very thin endozonal walls which thicken irregularly in the exozone. The acanthostyles are very abundant and frequently indent the autozooecial apertures producing a petaloid shape. Mesozooecia are common and have abundant diaphragms.

Stigmatella has not previously been described from Great Britain, although it is well known from North America and the U.S.S.R. *Stigmatella foordi* (Nicholson, 1889) from the Ordovician of Estonia has similar abundant acanthostyles which indent the autozooecial apertures. *S. foordi* can be distinguished by the hemispherical colony form, smaller acanthostyles, straight mesozooecia and less extensive thickening of the exozonal walls.

S. spinosa Ulrich & Bassler (Ulrich & Bassler 1904: pl. ix, figs 5–8; see also Bork & Perry 1968: pl. 48, figs 3–5), described from the Middle Ordovician of Iowa, has an irregularly thickened exozone which is similar to that of *S. oakleyi*. It differs from the Welsh species by having a greater number of diaphragms in the autozooecia, fewer mesozooecia, and acanthostyles which do not inflect the autozooecial apertures.

Genus *PEDROGOPORA* nov.

TYPE SPECIES. *Pedrogopora taylori* sp. nov.; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

NAME. After Llanbedrog (= Church of St Pedrog), the nearest town to the type locality.

DIAGNOSIS. Colony ramose. Autozooecia parallel to branch axis in endozone, then curve abruptly outwards to intersect zoarial surface. Walls very thin and wavy in the endozone, greatly thickened in exozone. Autozooecia compressed rounded-polygonal, vesicular appearence in transverse section, oval-circular to slightly petaloid in shallow tangential section. Oval mesozooecia common, some with extremely thin walls, originating in outer endozone and inner exozone. Diaphragms rare in autozooecia, present in exozonal mesozooecia. Acanthostyles abundant in exozone.

REMARKS. *Pedrogopora* is primarily characterized by its wall tructure. The autozooecia within the endozone have very hin walls and often have an unusual vesicular appearance. In the exozone the walls increase greatly in thickness. Mesozooecia often have exceptionally thin walls and have the ppearance of simple space-filling structures between the utozooecia (Fig. 6d). Wall microstructure is composed of teeply inclined, V-shaped laminae and zooecial wall boundries are dark and granular.

The genus is similar to *Leioclema* Ulrich, 1882 but the latter does not have such wide variation in wall thickness between the exozone and endozone. Thin-walled mesozooecia are also not recognized in *Leioclema*.

The monotypic genus is currently known only from the Upper Ordovician, at the type locality.

Pedrogopora taylori sp. nov. Figs 5–6, 8

HOLOTYPE. BMNH PD 2642; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

PARATYPES. BMNH PD 2646A, 2700, 8298–302; all from the same locality and horizon as the holotype.

NAME. For Dr P. D. Taylor of the Natural History Museum, for his work on bryozoans.

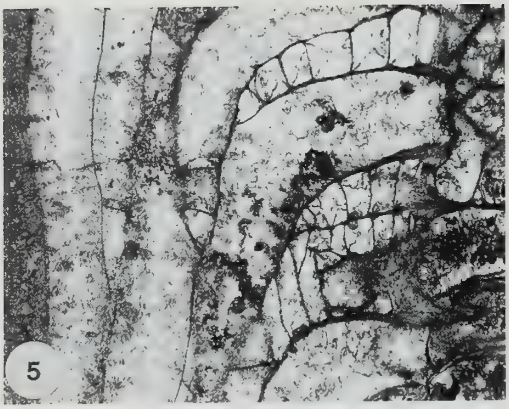
DIAGNOSIS. As for genus.

DESCRIPTION. Zoaria erect with cylindrical branches, on average 5·6 mm in diameter. Autozooecia are parallel to the branch axis within the endozone and then curve outwards abruptly in the exozone to meet the zoarial surface at 90°. Autozooecial walls within the endozone are exceptionally thin and slightly wavy. The exozone is usually wide with an average width of 1·67 mm. It is recognized by a thickening of the zooecial walls and a simultaneous change in zooecial orientation. Autozooecia all originate in the endozone where they have an irregular, compressed, rounded-polygonal shape in transverse section; some autozooecia have a vesicular appearance. They become oval-circular to slightly petaloid in the exozone, as seen in tangential sections of branches. Autozooecial diameters average 0·24 mm × 0·36 mm within the exozone. Diaphragms are rare or absent in autozooecia and, when present, only one or two are found in the exozone. They are basal diaphragms deflected orally at their junctions with the zooecial walls, and have laminae continuous with autozooecial linings.

Mesozooecia are common, originate in the outer parts of the endozone and inner parts of the exozone, and have an average diameter of 0·14 mm. Wall thickness varies considerably, and while some mesozooecia have a distinctly laminar wall, others have exceptionally narrow walls and appear to be simple space-filling structures between the autozooecia (Fig. 6d). Mesozooecia are oval in shallow tangential section, and contain orally-deflected basal diaphragms in the outer endozone and exozone. The diaphragms are spaced on average 0·09 mm apart and generally increase in thickness distally along the mesozooecium.

Acanthostyles are abundant with an average diameter of 0·06 mm and density of 7 per mm^2. They are long, originate deep in the exozone and can occasionally indent the autozooecial apertures to produce a petaloid shape. They are usually found at the junctions of three or more zooecia but

igs 1–4 *Stigmatella oakleyi* sp. nov.; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. Fig. 1, BMNH PD 2670 (paratype), longitudinal section, showing very thin endozonal walls, × 20. Fig. 2, BMNH PD 2641 (**holotype**); 2a, transverse section, × 25; 2b, tangential section, showing large acanthostyles inflecting the autozooecia, × 45; 2c, tangential section, showing microstructure, × 110. Fig. 3, BMNH PD 2664 (paratype), tangential section, showing maculae consisting predominantly of mesozooecia, × 35. Fig. 4, BMNH PD 2670 (paratype); 4a, longitudinal section showing interzoarial overgrowth, × 28; 4b, longitudinal section showing 'cyst' structures in the exozone, × 50; 4c, longitudinal section showing a cluster of 'cyst' structures in the exozone, × 145.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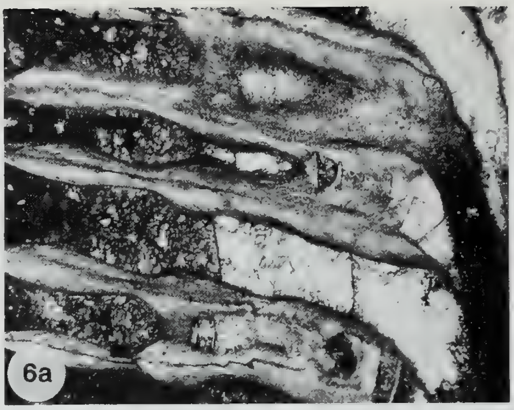
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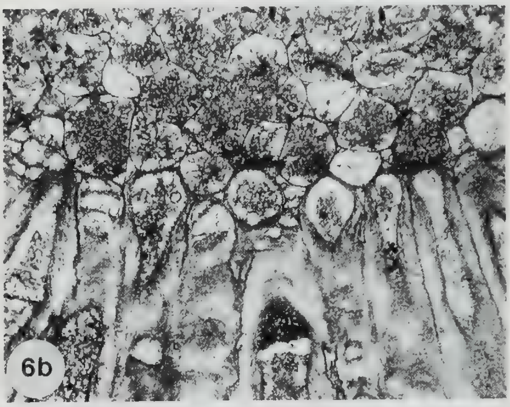
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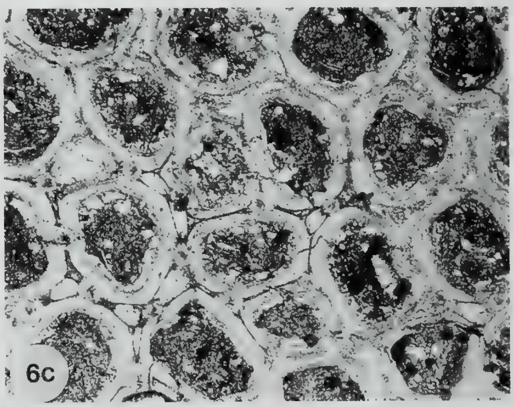
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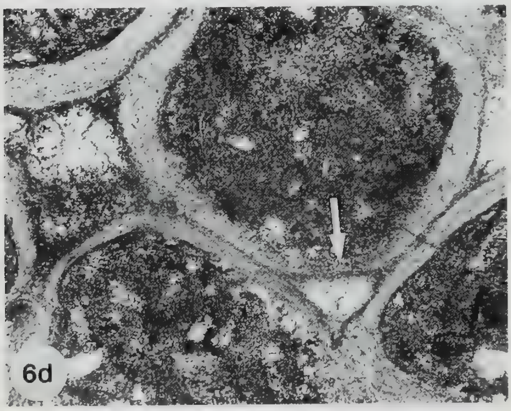
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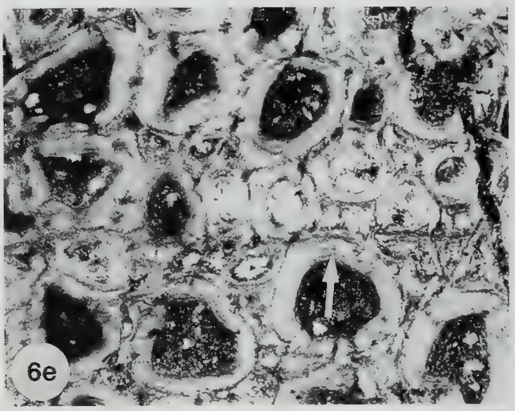
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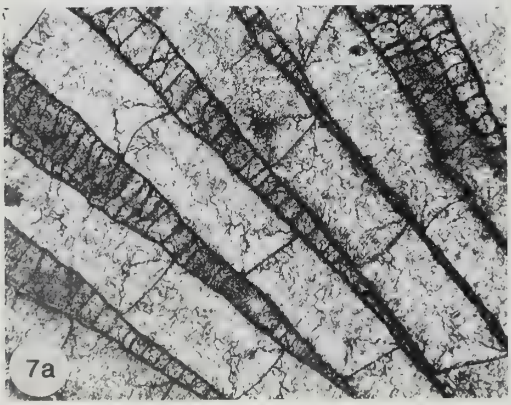
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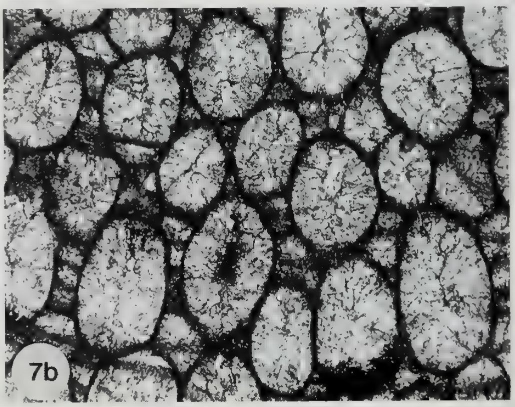
7b

also occur in the walls between adjacent zooecia. A narrow hyaline calcite core is surrounded by steeply dipping conical laminae.

Autozooecial wall thickness averages 0·14 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae and zooecial wall boundaries are dark and granular. Some zooecia, especially mesozooecia, are infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Maculae composed of mesozooecia have been recognized in shallow tangential thin section in one specimen (PD 2642, Fig. 6e). Intrazoarial overgrowths have been recognized in several specimens (e.g. PD 8302) and they are composed of outer endozone and exozonal elements.

Remarks. This is the only species of *Pedrogopora* so far recognized. Within the species there is variation in the width of the endozone from 2·28 mm (in the type specimen PD 2642) to 0·86 mm (in PD 8299). The thin-walled mesozooecia are not observed in all specimens.

Family **HALLOPOROIDAE** Bassler, 1911

Genus ***DIPLOTRYPA*** Nicholson, 1879

Diplotrypa pseudopetropolitana Astrova, 1965 Fig. 7

1948 *Diplotrypa petropolitana* (Nicholson); Astrova: 16; pl. 2, figs 4–5; pl. 3, fig. 1.

1965 *Diplotrypa pseudopetropolitana* Astrova: 189; pl. 30, fig. 3; pl. 31, fig. 1.

1970 *Diplotrypa pseudopetropolitana* Astrova; Nekhorosheva: 75; pl. 1, fig. 4.

Holotype. H No 1244/40, Yugorskiy Stage (Caradoc), Pai-Khoi and Vaigach Id, Zapadno-Arktichenskoy, U.S.S.R. (Astrova 1948).

Material examined. BMNH PD 2626, Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314); D 28581, 'Bala Limestone', Gelli Grîn, Gwynedd, Wales.

Description. Zoaria are hemispherical in the fragmentary specimens examined. Autozooecia originate at the centre of the colony and curve outwards towards the zoarial surface. Autozooecial walls are straight and thin throughout most of the colony. There is no differentiation between endozone and exozone. The autozooecia are rounded in transverse section throughout the zoaria, with an average maximum diameter of 0·44 mm in the exozone. Diaphragms are present, although not abundant, along the whole length of the autozooecia. These are basal diaphragms deflected orally at their junctions with the zooecial walls.

Mesozooecia are numerous and originate throughout the colony. They are rounded in transverse section and have a maximum diameter which averages 0·16 mm. Mesozooecia contain very abundant, orally-deflected, basal diaphragms along their entire length; they are spaced on average 0·07 mm apart and increase very slightly in thickness at the distal end of the mesozooecia. Cystiphragms are occasionally present instead of diaphragms throughout the mesozooecia; they occur on alternating sides of the mesozooecia.

Autozooecial walls are thin and the wall microstructure is composed of inclined U-shaped laminae. Zooecial boundaries are wide granular regions, most clearly seen in shallow tangential sections.

Remarks. *Diplotrypa pseudopetropolitana* Astrova, 1965 has been described previously from Vaigach Id and Pai-Khoi in the Soviet Union by Astrova (1965) and Nekhorosheva (1970). Astrova distinguished the new species from the similar *D. petropolitana* (Nicholson, 1879) by the presence of rounded (not polygonal) autozooecial apertures and more abundant mesozooecia. *D. petropolitana* is a frequently described species, with several recorded varieties and subspecies. It is very variable, especially in the number and distribution of diaphragms within the autozooecia. *Hallopora*? *dybowskii* Bassler, 1911 is extremely similar to *D. petropolitana*, as Bassler himself remarked (1911: 336), and should be synonymized.

D. nontabulata sp. nov. (below) is also described from Llanbedrog. It differs from *D. pseudopetropolitana* by having rare diaphragms within the autozooecia.

Only one species of *Diplotrypa* has been previously described from Great Britain. This is *D. hvergelmi* McNamara, 1978 from the Applethwaite Beds (Ashgill) of Troutbeck in the Lake District. This species has sinuous walls, with diaphragms widely spaced throughout the zooecia.

Diplotrypa nontabulata sp. nov. Figs 8–9

?1968 *Diplotrypa* sp. Bork & Perry: 340; pl. 45, figs 1–3.

Holotype. BMNH PD 8175; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

Paratypes. BMNH PD 2697, 2719, 8174; all from same locality and horizon as the holotype.

Other occurrence. ? Guttenberg Formation (Caradoc), Guttenberg, Iowa, U.S.A.

Name. In consideration of the lack of diaphragms within the autozooecia.

Diagnosis. Colony hemispherical. Zooecia have straight, thin walls and are budded from the basal lamina. No differentiation between endozone and exozone is recognized. Autozooecia large, polygonal-circular in transverse section throughout zoaria. Polygonal mesozooecia present. Diaphragms very rare in autozooecia, abundant in mesozooecia,

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Figs 5–6 *Pedrogopora taylori* gen. et sp. nov.; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. Fig. 5, BMNH PD 8302 (paratype), longitudinal section, showing thin endozonal walls, × 28. Fig. 6, BMNH PD 2642 (**holotype**); 6a, longitudinal section, × 35; 6b, transverse section, showing compressed rounded-polygonal autozooecia in the endozone, × 28; 6c, tangential section, × 28; 6d, tangential section, showing thin-walled space-filling mesozooecia, × 110; 6e, tangential section, showing maculae, × 28.

Fig. 7 *Diplotrypa pseudopetropolitana* Astrova, 1965; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. BMNH PD 2626; 7a, longitudinal section, × 28; 7b, tangential section, × 35.

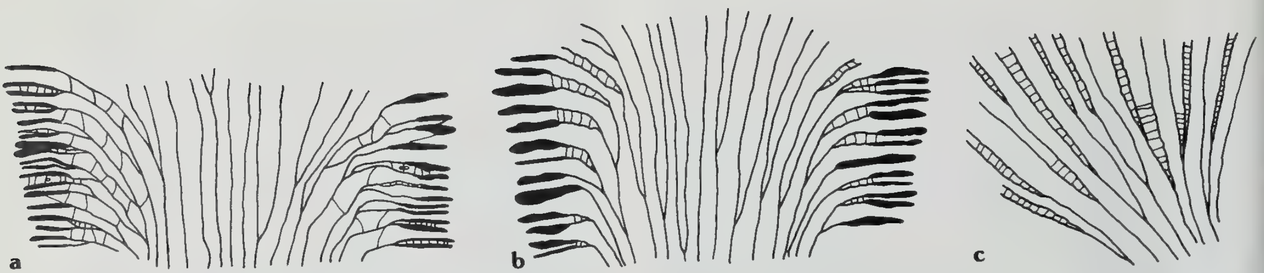

Fig. 8 Longitudinal sketches of the new species described from the Llanbedrog Mudstones. a, *Stigmatella oakleyi*. b, *Pedrogopora taylori*. c, *Diplotrypa nontabulata*.

often constricting chamber width, producing beaded appearance.

Description. Zoaria massive and hemispherical, on average 9·5 mm in diameter. All specimens are fragmentary and no bases are preserved. Autozooecia bud from the basal lamina and curve upwards to the zoarial surface. Autozooecial walls are straight throughout the zoaria, and no differentiation between exozone and endozone can be distinguished. Autozooecia are large with an average diameter of 0·38 mm × 0·44 mm, and are polygonal-circular in transverse section throughout the colony. Diaphragms are absent or very rare in autozooecia; if present they occur in the outermost parts of the autozooecia.

Mesozooecia present, often in abundance, in all zoaria and originate throughout the colony. Maximum diameter averages 0·23 mm; however, there is a large range (0·08–0·44 mm). Mesozooecia are polygonal, often triangular or rectangular, frequently positioned at the autozooecial corners. Mesozooecia contain abundant diaphragms along their entire length. These are basal diaphragms deflected orally at their junctions with the zooecial walls, and spaced on average 0·16 mm apart in the endozone and 0·15 mm in the exozone. Mesozooecia are often constricted at the position of the diaphragms, producing a beaded appearance in longitudinal section.

Autozooecial walls are thin which, combined with poor preservation, results in difficulties in distinguishing wall microstructure. In one specimen (PD 8174) the walls thicken very slightly close to the zoarial surface, reaching a thickness of 0·032 mm. There is an indistinct dark band at the centre of the wall, bordered by lighter bands on either side which have a vague laminar appearance. Within the main body of the zoarium the walls are dark and structureless.

Remarks. *Diplotrypa nontabulata* sp. nov. is primarily characterized by the rare diaphragms within the autozooecia, small mesozooecia with abundant diaphragms and thin straight walls.

Bork & Perry (1968) described '*Diplotrypa* sp.', from the Guttenberg Formation (Caradoc), Guttenberg, Iowa, U.S.A., which was characterized by the rare autozooecial diaphragms and a small number of mesozooecia with very abundant diaphragms. They only had one specimen and did not consider that a species could be based on a single zoarium. It is certainly very similar to *D. nontabulata* sp. nov., but the Welsh species has more abundant mesozooecia. The Iowa specimen is tentatively assigned to *D. nontabulata* here; the smaller number of mesozooecia may simply reflect intraspecific variation.

Bork & Perry (1968: 341) listed three species of *Diplotrypa* which had few diaphragms: *D. catenulata* Coryell (1921: pl. 10, figs 6, 7) with crenulated zooecial walls; *D. abnormis* (Modzalevskaya) (*in* Astrova, 1965: pl. 28, fig. 1b) with widely-spaced, curved diaphragms throughout the autozooecia; and *D. westoni* Ulrich (1889: pl. 8, figs 4–4b) with occasional diaphragms within the autozooecia.

Genus ***HALLOPORA*** Bassler, 1911

Hallopora cf. ***tolli*** Bassler, 1911 Fig. 10

Material examined. BMNH PD 2666; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

Description. Zoarium erect with small cylindrical branches, on average 5 mm in diameter. Autozooecia are parallel to the branch axis within the endozone and curve outwards gently in the outer endozone to meet the zoarial surface at 80°–90°. The autozooecia within the endozone have thin straight walls. The exozone is narrow with an average width of 0·86 mm. It is recognized by a slight thickening of the zooecial walls and a simultaneous change in zooecial orientation. Autozooecia all originate in the endozone where they are polygonal-rounded in transverse section, becoming oval-rounded in the exozone

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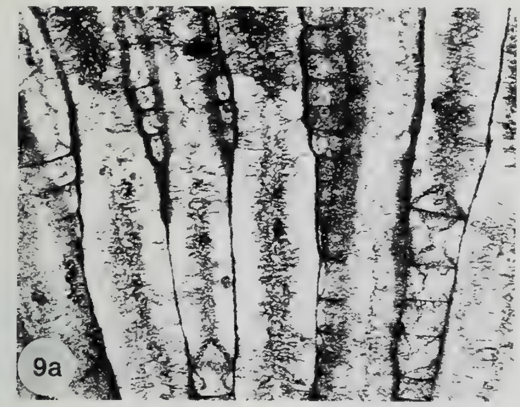
Fig. 9 *Diplotrypa nontabulata* sp. nov.; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. BMNH PD 8175 (**holotype**); 9a, longitudinal section, showing the lack of diaphragms within the autozooecia, × 25; 9b, tangential section, × 35.

Fig. 10 *Hallopora* cf. *tolli* Bassler, 1911; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. BMNH PD 2666; 10a, longitudinal section, × 35; 10b, transverse section, × 35; 10c, tangential section, × 50.

Figs 11–12 *Eridotrypa* cf. *kilbartiensis* Pushkin (*in* Ropot & Pushkin, 1987); Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. Fig. 11, BMNH PD 2722; 11a, longitudinal section showing the exceptionally thickened exozonal walls, × 50; 11b, transverse section, showing large autozooecia in the centre of the endozone, × 50. Fig. 12, BMNH PD 2691, tangential section, × 80.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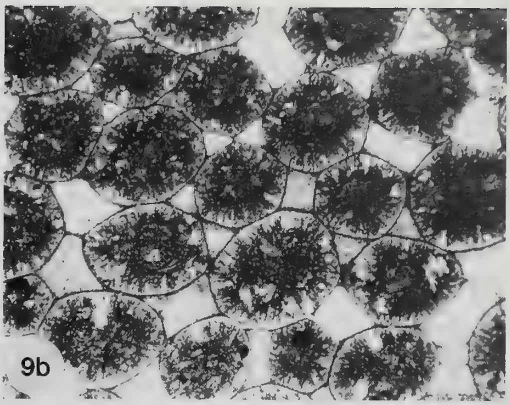
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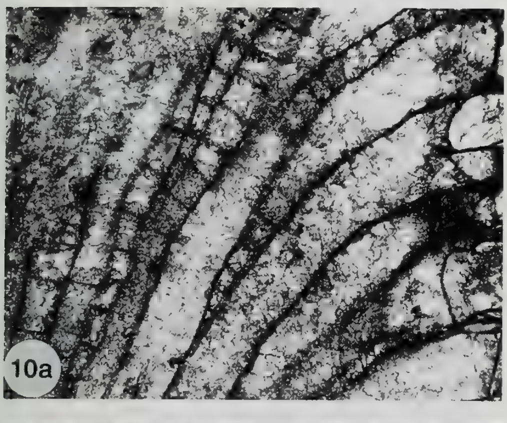
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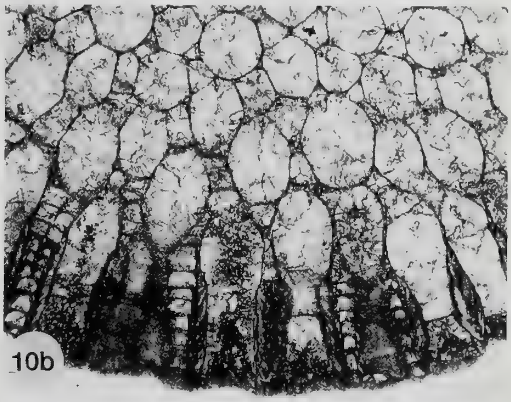
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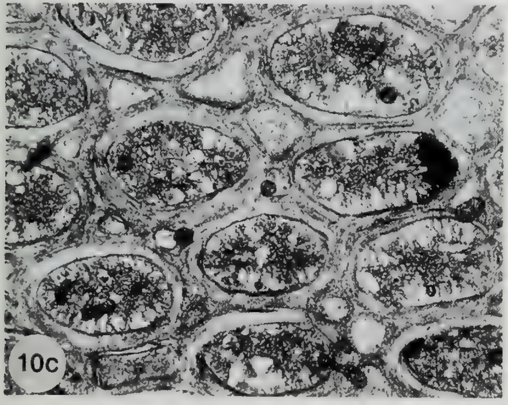
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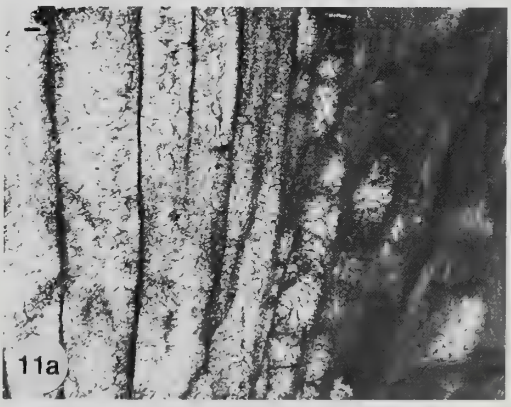
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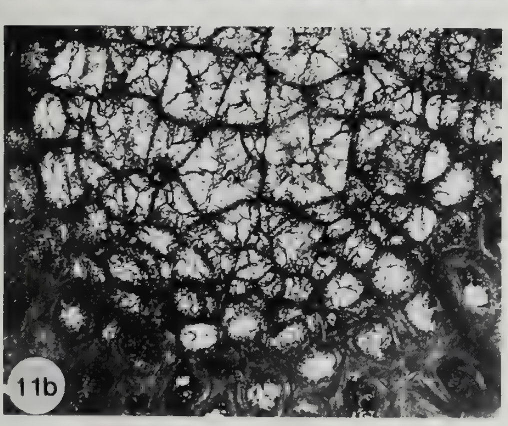
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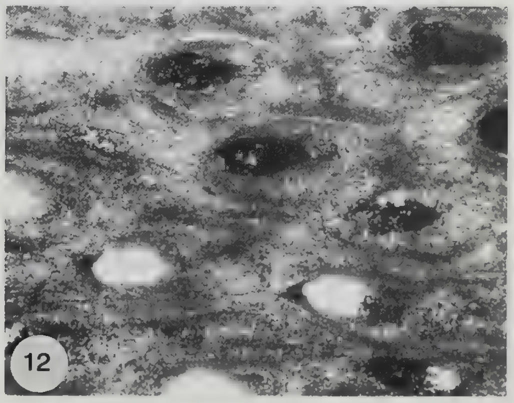
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as seen in shallow tangential sections of branches. Autozooecial diameters average 0·23 mm × 0·31 mm within the exozone. Diaphragms in the endozone are not abundant and are spaced on average 0·21 mm apart. They are spaced 0·11 mm apart in the exozone. Only one or two diaphragms are found at the outer ends of autozooecia in the exozone. All of these diaphragms are basal, deflected orally at their junctions with the zooecial walls, and their laminae are continuous with autozooecial linings.

Mesozooecia are common, originating in the outer part of the endozone and having a maximum diameter which averages 0·13 mm in the exozone. They are circular to rounded-polygonal in shallow tangential sections. Mesozooecia contain abundant orally-deflected basal diaphragms, spaced on average 0·06 mm apart, which occasionally increase in thickness distally along the mesozooecia.

Autozooecial wall thickness averages 0·08 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae. The zooecial wall boundaries are wide, granular areas, most clearly seen in shallow tangential section. Some zooecia are infilled with laminar calcite close to the colony surface. In longitudinal section this infilling consists of broad U-shaped laminae.

REMARKS. The single specimen described here is characterized by the ramose colony form and thin-walled autozooecia. Autozooecial apertures are polygonal-rounded in transverse zoarial section and oval-rounded in shallow tangential zoarial section. Rounded-polygonal mesozooecia are common and originate in the endozone. Diaphragms are occasionally present in the outer autozooecia and are abundant in the mesozooecia.

Bassler (1911) described *Hallopora tolli* originally from the Jewe Limestone, Kuckers Shale and Kegal Limestone (Caradoc) of Estonia, and illustrated longitudinal and deep tangential sections. This species has long, straight mesozooecia with abundant diaphragms, similar to the Welsh specimen. The autozooecia are polygonal-rounded in tangential section (their shape in zoarial transverse section is not known). However, Bassler's section is very deep and is difficult to compare directly with that of the Welsh specimen. Fritz (1941) described *H. tolli* from the Whitehead Formation, Gaspé, Québec, Canada, but her description is not well illustrated. Bork & Perry (1967) tentatively described one fragmentary specimen as *H.* cf. *tolli* from the Guttenberg Formation (Caradoc) of Iowa, U.S.A. It differs from the specimen illustrated by Bassler in having thinner walls. Until the type material of *H. tolli* has been re-examined, the true nature of the species will remain obscure. Because of this the poorly preserved Welsh specimen is named *H.* cf. *tolli*.

Singh (1979) proposed the genus *Parvohallopora* for some species previously assigned to *Hallopora*. He distinguished the two genera on the basis of the following characteristics: in *Parvohallopora*, zooecia are of smaller diameter than in *Hallopora*; mural spines are absent in *Parvohallopora* but are present in the type species of *Hallopora*; mesozooecia are generally smaller in *Parvohallopora*; zooecia are polygonal in the endozone of *Parvohallopora*, whereas in *Hallopora* they are rounded to subrounded; cystose diaphragms are rare to absent in *Parvohallopora* but are more common in *Hallopora*; and the laminae of adjacent zooecia are broadly U/V-shaped in *Parvohallopora* and distinctly V-shaped in *Hallopora*.

The present specimen is assigned to *Hallopora*, despite the possession of certain characters attributed to *Parvohallopora*: the endozonal zooecia are polygonal-rounded and the mesozooecia are small, both characteristics of *Parvohallopora*. However, the occasional presence of diaphragms in the autozooecia and the V-shaped laminae in the zooecial walls are attributes of *Hallopora*. This seems to show that the distinction between the two genera is less clear-cut than Singh suggests.

Genus ***ERIDOTRYPA*** Ulrich, 1893

Eridotrypa cf. ***kilbartiensis*** Pushkin (*in* Ropot & Pushkin, 1987) Figs 11–12

MATERIAL EXAMINED. BMNH PD 2691, 2720, 2722; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

DESCRIPTION. Zoaria erect with very narrow cylindrical branches, on average 2·5 mm in diameter. The three specimens from Llanbedrog are poorly preserved. Autozooecia are parallel to the branch axis within the endozone and then curve slightly in the exozone to meet the zoarial surface at 45°. The autozooecia within the endozone have thin, straight walls. The exozone is narrow with an average width of 0·76 mm; it is recognized by an extensive thickening of the zooecial walls. Autozooecia all originate in the endozone and are polygonal in transverse section, becoming oval in the exozone as seen in tangential sections of branches. In transverse section the autozooecia are twice the diameter in the inner endozone than in the outer endozone. Autozooecial diameters average 0·10 mm × 0·12 mm within the exozone. Diaphragms are present in the outer endozone and exozone, spaced on average 0·11 mm apart. These basal diaphragms are all deflected orally at their junctions with zooecial walls.

No mesozooecia have been conclusively identified in the three specimens examined.

Acanthostyles have been observed in the exozone of one specimen (PD 2722). They are short and composed of a hyaline calcite core surrounded by steeply dipping laminae.

Autozooecial walls are thick in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae (microstructure is slightly indistinct due to the age and thickness of the thin sections). Zooecial boundaries have not been distinguished. Some zooecia are infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

REMARKS. The three poorly preserved specimens from Llanbedrog assigned to *Eridotrypa* cf. *kilbartiensis* Pushkin are characterized by their slender branches, and autozooecial walls which are thin and straight in the endozone and thicken in the exozone. Autozooecial apertures are large and polygonal in transverse section, small and oval in shallow tangential sections. Diaphragms are present in the exozonal autozooecia and occasionally in the endozone.

The specimens are very similar to *E. kilbartiensis* Pushkin (*in* Ropot & Pushkin, 1987), described from the Oanduskii Stage (Caradoc), White Russia. *E. kilbartiensis* has thin, straight walls in the endozone which thicken extensively in the exozone (Ropot & Pushkin 1987: pl. 14, figs 3a, b). The major difference is the greater number of diaphragms in the exozone of the Welsh specimens. There may be range of variability within the species, but until further material can be examined, the Welsh material is tentatively identified as *E.* cf. *kilbartiensis*.

Family **MONTICULIPORIDAE** Nicholson, 1881

Genus ***PRASOPORA*** Nicholson & Etheridge, 1877

Prasopora grayae Nicholson & Etheridge, 1877 Figs 13–15

1877 *Prasopora grayae* Nicholson & Etheridge: 392.
1881 *Monticulipora (Prasopora) grayae* Nicholson & Etheridge; Nicholson: 203; figs 42–43.
1987 *Prasopora grayae* Nicholson & Etheridge; Ropot & Pushkin: 190; pl. 22, fig. 4.

LECTOTYPE. Selected herein from the type locality, BMNH D 32195 (a longitudinal thin section); Craighead Beds (Upper Ordovician), Craighead Quarry, Ayrshire, Scotland. This specimen is possibly one of the original ones figured by Nicholson & Etheridge (1877: fig. D). A tangential section (BMNH D 32196) may be part of the same colony.

MATERIAL EXAMINED. BMNH PD 2627, 2699; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

OTHER OCCURRENCE. Kukrusean Stage (Upper Llandeilo/Early Caradoc), White Russia, U.S.S.R.

DESCRIPTION. Zoaria hemispherical, on average 11 mm in diameter. The basal lamina, observed only in thin section, is thin and the microstructure indistinct. Autozooecia all originate at the base of the colony and gently curve upwards to the zoarial surface. Autozooecial walls are straight and quite thin throughout most of the colony. No differentiation between the endozone and the exozone can be recognized. In the periphery of the colony the autozooecia are rounded-polygonal in shallow tangential sections, with average diameters of 0·41 mm × 0·31 mm. Diaphragms and cystiphragms are common throughout the autozooecia, occurring together or alone. The diaphragms are basal and are all deflected orally at their junctions with the zooecial walls. The diaphragms are thin and spaced on average 0·1 mm apart in the endozone and 0·12 mm apart in the exozone. Cystiphragms are very abundant, usually present with diaphragms. They occur either on both sides of the autozooecia or confined to one side; this side, however, is not constant throughout the colony and they may be arranged centripetally.

Mesozooecia are numerous, and originate in the inner parts of the colony. They are rounded in transverse section and have a maximum diameter which averages 0·13 mm. Mesozooecia contain abundant orally-deflected diaphragms along their entire length. The diaphragms are spaced on average ·06 mm apart.

Autozooecial walls are thin throughout the colony. Wall microstructure is composed of inclined U-shaped laminae which may, however, be hard to distinguish. Zooecial boundaries are indistinct dark regions.

EMARKS. *Prasopora grayae* is characterized by the hemipherical colony form; autozooecial apertures which are ounded-polygonal in shallow tangential zoarial sections; iaphragms and cystiphragms which are very abundant in e autozooecia; and common diaphragms in the small esozooecia.

P. grayae was originally described from the Craighead Beds of Girvan by Nicholson & Etheridge (1877). Abundant specimens of this species are available for study at the Natural History Museum. Although zoaria from Scotland are larger than the Welsh specimens, zooecial apertures are of similar size. *P. grayae* has also been described from the Kukrusean Stage, White Russia, U.S.S.R, by Ropot & Pushkin (1987).

The lectotype (Fig. 13) of *P. grayae* is herein selected from the original 'Gray' collection described by Nicholson & Etheridge (1877). This particular colony has abundant 'brown-bodies' within the autozooecia (Figs 13a, c). These are granular deposits of iron oxide or pyrite, which are considered to represent the fossilized remains of organic material (Boardman & Cheetham, 1983).

P. insularis Ulrich var. *estonica*, described by Modzalevskaya (1953: 106) from the western Russian Platform, is similar to *P. grayae* but differs in having more abundant cystiphragms within the autozooecia and fewer diaphragms. *Prasopora* has been commonly recognized in North America (e.g. Ross, 1967), but the species *P. grayae* has never been recorded.

Prasopora thorali Prantl, 1940 has also been recognized from Llanbedrog: see below. It differs from *P. grayae* in having fewer mesozooecia and larger, less abundant cystiphragms.

Prasopora thorali Prantl, 1940 Figs 16–17

1940 *Prasopora thorali* Prantl: 89, figs 2, 3; pl. 1, fig. 10.
1948 *Prasopora thorali* Prantl; Dreyfuss: 42; pl. 1, figs 1–9.
1948 *Prasopora thorali* var. *elliptica* Dreyfuss: 25.

HOLOTYPE. Illustrated in Prantl (1940: pl. 1, fig. 10); east of Grange du Pin, Herault (Ashgill), Montagne Noire (Languedoc).

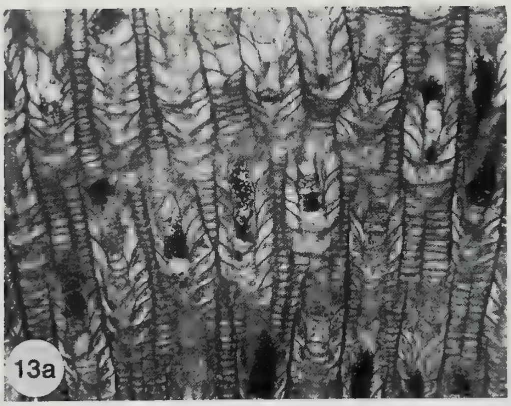
MATERIAL EXAMINED. BMNH PD 2687, 2689; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

DESCRIPTION. Zoaria hemispherical, on average 30 mm in diameter. Only fragmentary specimens of this species are known from Wales and no surface detail is preserved.

Autozooecia all originate at the base of the colony and gently curve upwards to the zoarial surface. Autozooecial walls are straight and quite thin throughout most of the colony.

No differentiation between endozone and exozone can be recognized. The autozooecia are polygonal in shallow tangential sections, with an average diameter of 0·35 mm × 0·43 mm. Diaphragms and cystiphragms are common throughout the autozooecia, occurring together or alone. The diaphragms are basal and are all deflected orally at their junctions with the zooecial walls. The diaphragms are thin and spaced on average 0·17 mm apart in the endozone and 0·14 mm in the exozone. Cystiphragms are very abundant, usually present with diaphragms. They are almost always confined to one side of the autozooecia, but which side is not, however, constant throughout the colony. The cystiphragms may be centripetally arranged with respect to the maculae.

Mesozooecia are present, although very rare, and originate in the inner parts of the colony. They are polygonal in transverse section and have a maximum diameter which averages 0·14 mm. Mesozooecia contain abundant orally deflected diaphragms along their whole length. The diaphragms are spaced on average 0·1 mm apart.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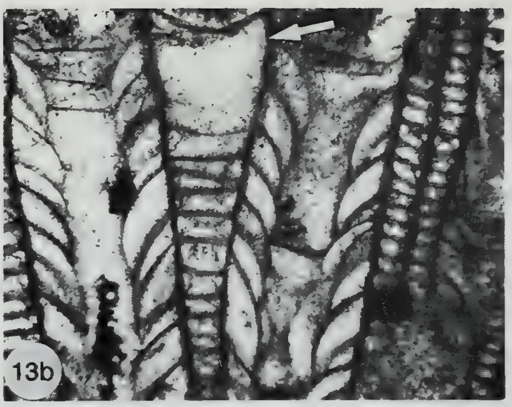
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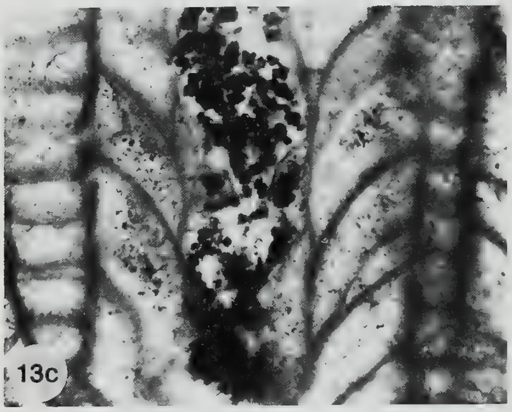
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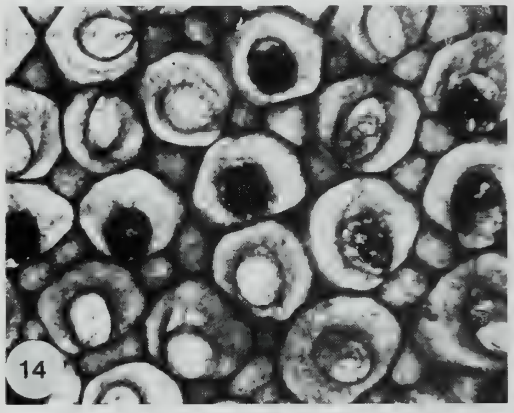
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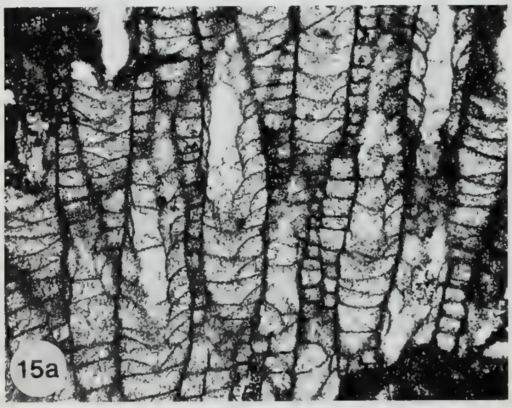
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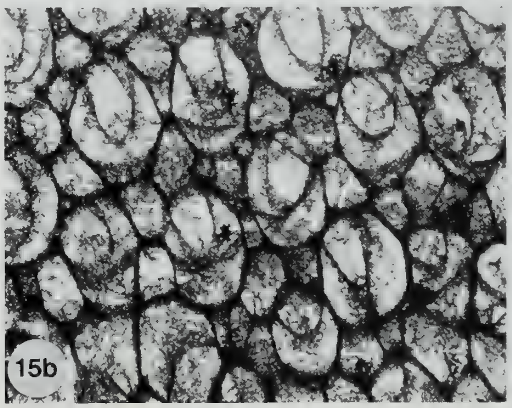
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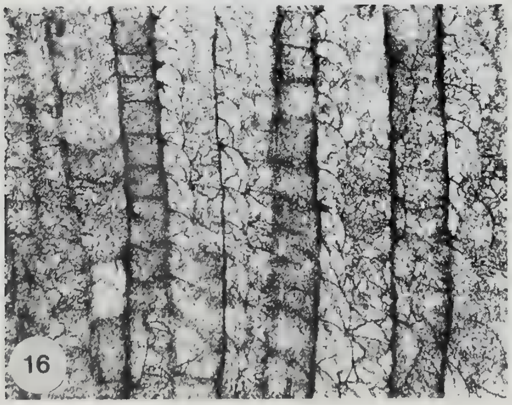
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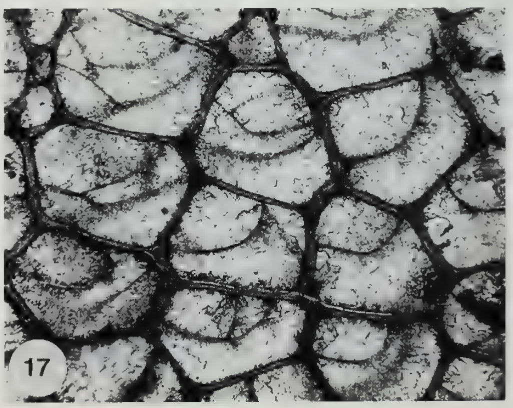

17

Autozooecial wall thickness averages 0·03 mm at the periphery of the colony. Wall microstructure is composed of inclined U-shaped laminae, and zooecial boundaries are dark and granular.

REMARKS. *Prasopora thorali* was first described by Prantl (1940) from the Upper Ordovician of the Montagne Noire in France. The species is characterized by a hemispherical to subconical colony form and subpolygonal autozooecial apertures (0·36–0·39 mm in diameter). Maculae are present and contain slightly larger autozooecia than in the rest of the colony. Cystiphragms are present in autozooecia and generally form continuous rows on one side of zooecia (three cystiphragms per mm). Diaphragms are commonly present in conjunction with the cystiphragms or without them. Zooecial walls are thin throughout the colony. Mesozooecia are rare and have abundant diaphragms (4–6 per mm). Small, indistinct acanthostyle-like structures have been recognized.

The measurements of the specimens from Llanbedrog overlap those from France, although the former generally have a larger range.

Dreyfuss (1948: 25) described *P. thorali* var. *elliptica*, which differed from *P. thorali* by having more numerous regular cystiphragms in the autozooecia. No illustrations were provided and the number of cystiphragms cited falls within the present extended range, so this variety is placed in synonymy with *P. thorali*.

Genus ***MESOTRYPA*** Ulrich, 1895

Mesotrypa sp. Fig. 18

MATERIAL EXAMINED. BMNH PD 8297; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

DESCRIPTION. Zoarium hemispherical, on average 8 mm in diameter. No exterior or basal details are preserved on the one known specimen. Autozooecia bud from the basal laminae and curve outwards to the zoarial surface; new zooecia are also intercalated above the basal laminae. The autozooecial walls are straight and thin throughout most of the colony. At the periphery of the colony the autozooecia are rounded-polygonal in shallow tangential sections, with an average maximum diameter of 0·34 mm. Diaphragms are very rare; only one has been recognized and is located in the outer part of an autozooecium.

Mesozooecia are very abundant and originate throughout the colony. They are polygonal, often triangular, in transverse section and have a maximum diameter which averages 0·17 mm. Mesozooecia contain abundant orally-deflected basal diaphragms throughout their length. The diaphragm laminae are continuous with autozooecial linings. They are spaced on average 0·12 mm apart in the endozone and 0·11 mm in the exozone, often increasing in thickness towards the distal end of the mesozooecia. Mesozooecia are often constricted at the position of the diaphragms, producing a beaded appearance in longitudinal section.

Acanthostyles are abundant and have an average diameter of 0·04 mm. They are located throughout the colony, having a greater abundance in the outer portions. They can indent autozooecial walls and in longitudinal section acanthostyles are observed protruding into the zooecia. A hyaline calcite core is surrounded by steeply dipping laminae.

Autozooecial walls are thin at the periphery of the colony. Wall microstructure is composed of inclined U-shaped laminae, and zooecial boundaries are indistinct. Walls are disrupted by the numerous acanthostyles making the microstructure difficult to distinguish.

REMARKS. Only one specimen of the genus *Mesotrypa* has been identified from the Llanbedrog Mudstones. This specimen is characterized by the hemispherical colony form, large autozooecia with thin straight walls, a rounded-polygonal aperture in tangential section and common mesozooecia. Diaphragms are rare in the autozooecia and common in mesozooecia. Acanthostyles are large and present throughout the colony.

Two species of *Mesotrypa* have been previously described from the Welsh Basin. *Mesotrypa lens* (M^c^Coy, 1850) was described by Spjeldnaes (1957:368) from the Caradoc Series of Horderly West, Shropshire. In the description of this species the absence of acanthostyles was noted. This suggests that the specimens may not belong to the genus *Mesotrypa*. A re-examination of these specimens is required. Ross (1963: 6) identified a new species, *M. bulmani*, from the Hoar Edge Group (Caradoc Series) of Shropshire. This species differs primarily from the Llanbedrog species in the presence of numerous diaphragms within the autozooecia and the sparse mesozooecia.

Mesotrypa strumaeformis, described by Pushkin (*in* Ropot & Pushkin, 1987: 156) from the Oanduskii and Rakverskii Stages (Middle Caradoc), Yuzhnoi, Pribaltiki, U.S.S.R., has similarities with the specimen from Llanbedrog. Diaphragms are absent in all the autozooecia, and the zooecia have similar diameters in both taxa. The major difference is the size of the acanthostyles which are up to three times larger in the Welsh specimen than in *M. strumaeformis*.

Suborder **CERAMOPORINA** Bassler, 1913
Family **CERAMOPORIDAE** Ulrich, 1882

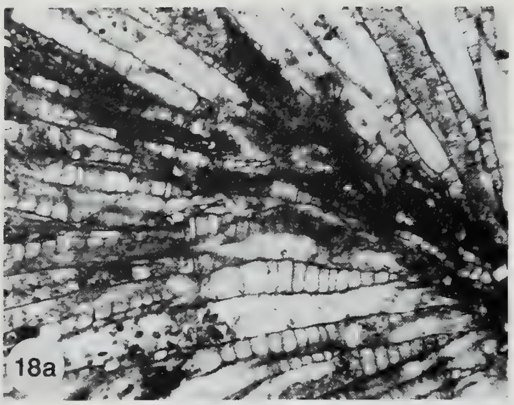
Genus ***CERAMOPORELLA*** Ulrich, 1882

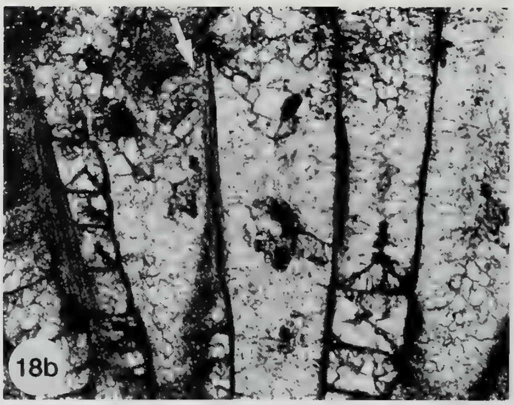
Ceramoporella distincta Ulrich, 1890 Fig. 19

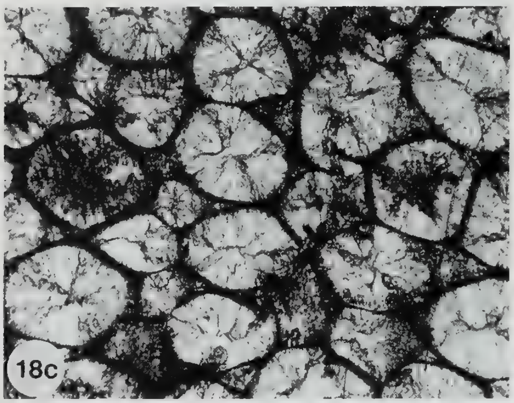
1890 *Ceramoporella distincta* Ulrich: 464; pl. 39, figs 6, 6a.
1908 *Ceramoporella distincta* Ulrich; Cumings: 799; pl. 10, fig. 7; pl. 11, figs 2, 2a.

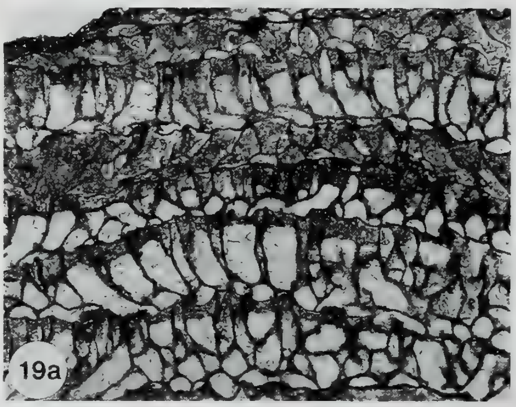
Figs 13–15 *Prasopora grayae* Nicholson & Etheridge, 1877; Figs 13–14, Craighead Beds (Upper Ordovician), Craighead Quarry, Ayrshire, Scotland. Fig. 13, BMNH D 32195 (**lectotype**, herein selected); 13a, longitudinal section, × 15; 13b, longitudinal section, showing an autozooecium developing from a mesozooecium-like polymorph, × 35; 13c, longitudinal section, showing a 'brown-body' within the autozooecium, × 85. Fig. 14, BMNH D 32196 transverse section, showing 'brown-bodies' within the autozooecia, × 85. Fig. 15, Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. BMNH PD 2699; 15a, longitudinal section, × 30; 15b, tangential section, × 45.

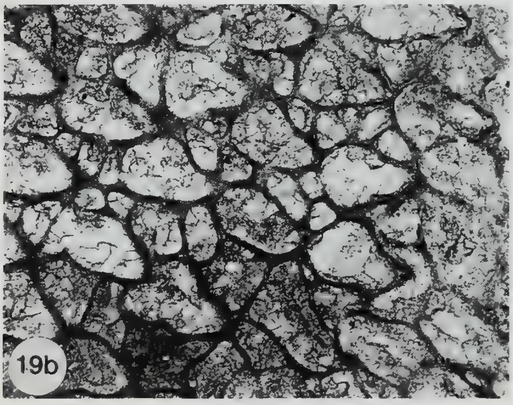
Figs 16–17 *Prasopora thorali* Prantl, 1940; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. Fig. 16, BMNH PD 2687, longitudinal section, × 30. Fig. 17, BMNH PD 2689, tangential section, × 45.











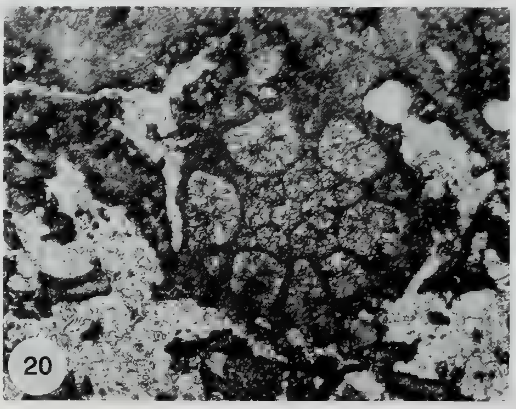


Fig. 18 *Mesotrypa* sp.; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. BMNH PD 8297; 18a, longitudinal section, × 15; 18b, longitudinal section, showing large acanthostyles in the exozone, × 40; 18c, tangential section, × 40.

Fig. 19 *Ceramoporella distincta* Ulrich, 1890; Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. BMNH PD 2642a; 19a, longitudinal section, showing the encrusting nature of the colony, × 15; 19b, tangential section, × 30.

Fig. 20 *Kukersella borealis* (Bassler, 1911); Llanbedrog Mudstones (Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales. BMNH PD 2652f, transverse section, × 70.

1909 *Ceramoporella distincta* Ulrich; Grabau & Shimer: 122.
1953 *Ceramoporella distincta* Ulrich; Bassler: figs 44, 2a, b.
1968 *Ceramoporella distincta* Ulrich; Utgaard: 1405; pl. 181, fig. 4; pl. 182, figs 1–3.
1973 *Ceramoporella distincta* Ulrich; Utgaard: figs 16, 23.
1984 *Ceramoporella distincta* Ulrich; Karklins: I89; pl. 38, figs 1, 4.
1991 *Ceramoporella distincta* Ulrich; Buttler: 100; pl. 6, figs 5–8.

LECTOTYPE. USNM 159710, McMiken strata of Eden Formation (Upper Ordovician), Cincinnati, U.S.A. (sel. Utgaard, 1968).

MATERIAL EXAMINED. PD 2642a, Llanbedrog Mudstones

(Soudleyan, Caradoc), near Llanbedrog, Gwynedd, Wales (SH 322314).

OTHER OCCURRENCES. Eden and Waynesfield Formation, Cincinnati; Brannon and Millersburg Members, Shermanian Stage, Lexington Limestone, Kentucky; Slade and Redhill Beds (Ashgill), near Whitland, Dyfed, Wales.

DESCRIPTION. Zoarium encrusting, consisting of up to five superimposed layers of autozooecia. The basal layers, observed in thin section, are thick (on average 0·79 mm) and the basal laminae of the layers have a laminated microstructure.

It is hard to distinguish endozone from exozone. In the endozone the autozooecia are slightly recumbent and zooecial walls are thin and straight. In the exozone the walls remain straight and zooecial apertures in shallow tangential section are circular-polygonal and on average 0·26 mm in diameter. Lunaria are abundant throughout the colony.

Diaphragms are occasionally present in the autozooecia. They are subterminal, aborally deflected and continuous with the zooecial linings. These diaphragms frequently occur at the same level in adjacent zooecia. Basal diaphragms are rare.

Small exilazooecia are present in the outer endozone and exozone. These contain no diaphragms and are rounded in shallow tangential section, on average 0·09 mm in diameter.

Communication pores have not been observed. Possible acanthostyle-like structures have been observed but not identified conclusively. The microstructure is hard to distinguish but appears to be laminar.

REMARKS. The species is characterized by the multilayered zoaria, thin autozooecial walls, sparse diaphragms and the presence of distinct lunaria. It is very similar to *Ceramoporella distincta* Ulrich, 1890, recently re-described by Karklins (1984: 189), from the McMiken Member, Eden Formation (Upper Ordovician), Cincinnati, Ohio, U.S.A. The main difference is that the specimens from Wales have fewer exilazooecia than those of North America. Similar specimens have been described from the Slade and Redhill Beds (Ashgill), near Whitland, Dyfed, Wales (Buttler 1991).

Order **CYCLOSTOMATA** Busk, 1852
Family **CROWNOPORIDAE** Ross, 1967

Genus ***KUKERSELLA*** Toots, 1952

Kukersella borealis (Bassler, 1911) Fig. 20

DESCRIPTION. Colony erect with narrow subcylindrical branches (average diameter 1·08 mm), arising from an encrusting base. Endozonal zooecia are very thin walled and are orientated parallel to the branch growth-direction to form an axial bundle. The endozonal zooecia only reach the colony surface at the distal growth tips. Abundant, closely spaced (0·09 mm) diaphragms occur throughout the length of the endozonal zooecia and are deflected orally at their junction with vertical interzooecial walls.

Exozonal zooecia surround the axial bundle of endozonal zooecia. They are thick-walled, average 0·48 mm in length and are connected by sparse interzooecial pores which penetrate interzooecial walls at levels close to the colony surface. Occasional diaphragms are developed at levels close to the colony surface; they are deflected orally where they meet the interzooecial walls. Frontal walls of exozonal zooecia have distal subcircular apertures with an average diameter of 0·15 mm and slight peristomes. The frontal walls are densely pseudoporous. The pseudopores are variable in size, but consistantly large, on average 0·02 mm in diameter. They are crater-like in external morphology, with funnel-shaped openings. The encrusting bases are composed entirely of exozonal wall material.

REMARKS. A redescription and complete synonymy list of *K. borealis* is given in Buttler, 1989.

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The biostratigraphical and evolutionary significance of *Alveolinella praequoyi* sp. nov. from Papua New Guinea

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SYNOPSIS. A primitive species of *Alveolinella*, intermediate between *Flosculinella bontangensis* (Rutten) and *Alveolinella quoyi* (d'Orbigny), is described as new from the Darai Limestone of Papua New Guinea. In the type section, it occurs through at least 50 m of Middle Miocene limestone referable to the upper part of Tf_1 and to Tf_2 in terms of the East Indies Letter Classification of the Tertiary. The biostratigraphical significance of this find is discussed, and mention made of the relevance of the new taxon to the evolutionary debate on punctuated equilibria versus secular change.

INTRODUCTION

Alveolinella praequoyi sp. nov. was discovered independently by the authors during examinations of the Darai Limestone between 1982 and 1987. On the basis of Australasian Petroleum Company collections studied in Melbourne, Adams (1984) referred to it as *A. fennemai* Checchia-Rispoli, and noted (1984: 59) that the specimen figured by Eames, Banner, Blow & Clarke (1962) as *A. fennemai* appeared to be intermediate between *Flosculinella* and *Alveolinella*. Wonders, working with material collected more recently by the British Petroleum Company, concluded that specimens from the Darai Limestone previously referred to *A. fennemai* should be described as new.

The material described in this paper was obtained from two samples collected from an unnamed river gorge, cut through the northeastern part of the Hides Anticline, Central Highlands, P.N.G. (Figs 1, 2). In this locality the species ranges through at least 50 m of limestone. Elsewhere, it may occur through up to 250 m of the Darai Limestone, which is *c.* 1,500 m thick. Additional material was obtained from other areas and localities; notably, traverses across the Darai and Orie anticlines, and samples collected during an earlier reconnaissance survey of the Tari area by the Australasian Petroleum Company (1955, unpublished report). See Fig. 1.

The present study is based mainly on randomly orientated thin sections, isolated specimens not being obtainable from the hard matrix of this limestone. However, a few orientated thin sections were prepared in the Natural History Museum from specimens seen on polished rock surfaces, using the method described by Hodgkinson & Margerum (1986).

Since recognizable planktonic foraminifera are rarely present in the shallow water facies of the Darai Limestone, the material described here is dated in terms of the East Indies Letter Classification of the Tertiary (*sensu* Adams, 1984, with minor modifications). Revised definitions of the relevant letter 'stages' are given below.

Tf_3: upper boundary defined by the extinction of *Lepidocyclina*. It should be noted that the Darai Limestone is disconformably/uncomformably overlain by deep-water shales of N17 age in the Hides Anticline (Fig. 2), and that the precise age of its uppermost beds is not known. *Lepidocyclina* seems to be absent from Tf_3 in this area for facies reasons.

Tf_2: upper boundary defined by the extinction of *Katacycloclypeus annulatus* K. Martin. It is possible, but not certain that *Flosculinella* may also range to the top of this division. Unfortunately, the Tf_2 limestones in the Papuan fold belt are often in shallow open marine facies without alveolinids.

Tf_1: upper boundary defined by the extinction of *Austrotrillina howchini* (Schlumberger) and/or *F. bontangensis* (Rutten).

Te_5 (Upper Te of Adams, 1970): upper boundary defined by the extinction of *Lepidocyclina (Eulepidina)* and/or *Spiroclypeus*.

Te_{1-4} (Lower Te of Adams, 1970): upper boundary defined by the extinction of *Vlerkina* [= *Heterostegina*, auctt.] *borneenis* (van der Vlerk) and *Miogypsinoides complanatus* (Schlumberger). Most authors draw this boundary at the first appearance of *Miogypsina*, but this is an unsatisfactory and dangerous procedure unless the species can be identified.

It is believed that three divisions of Tf_1 can be recognized in Papua New Guinea. Upper f_1 with *Austrotrillina howchini* (Schlumberger). *Flosculinella bontangensis* (Rutten) and *Alveolinella praequoyi* sp. nov.; middle f_1, a poorly fossiliferous unit, but typically containing *A. howchini* and *Flosculinella bontangensis*; and lower f_1 with *Miogypsinoides dehaarti* van der Vlerk and *Pseudotaberina malabarica* (Carter). These units are not, however, thought to be of regional (Indo–West Pacific) significance since their boundaries seem to be facies-controlled.

The Alveolinidae is a family of larger miliolacean foraminifera which originated in the Early Cretaceous (*Ovalveolina* and *Praealveolina*, Albian), and is represented in present-day tropical seas by *Borelis* and *Alveolinella*. Its

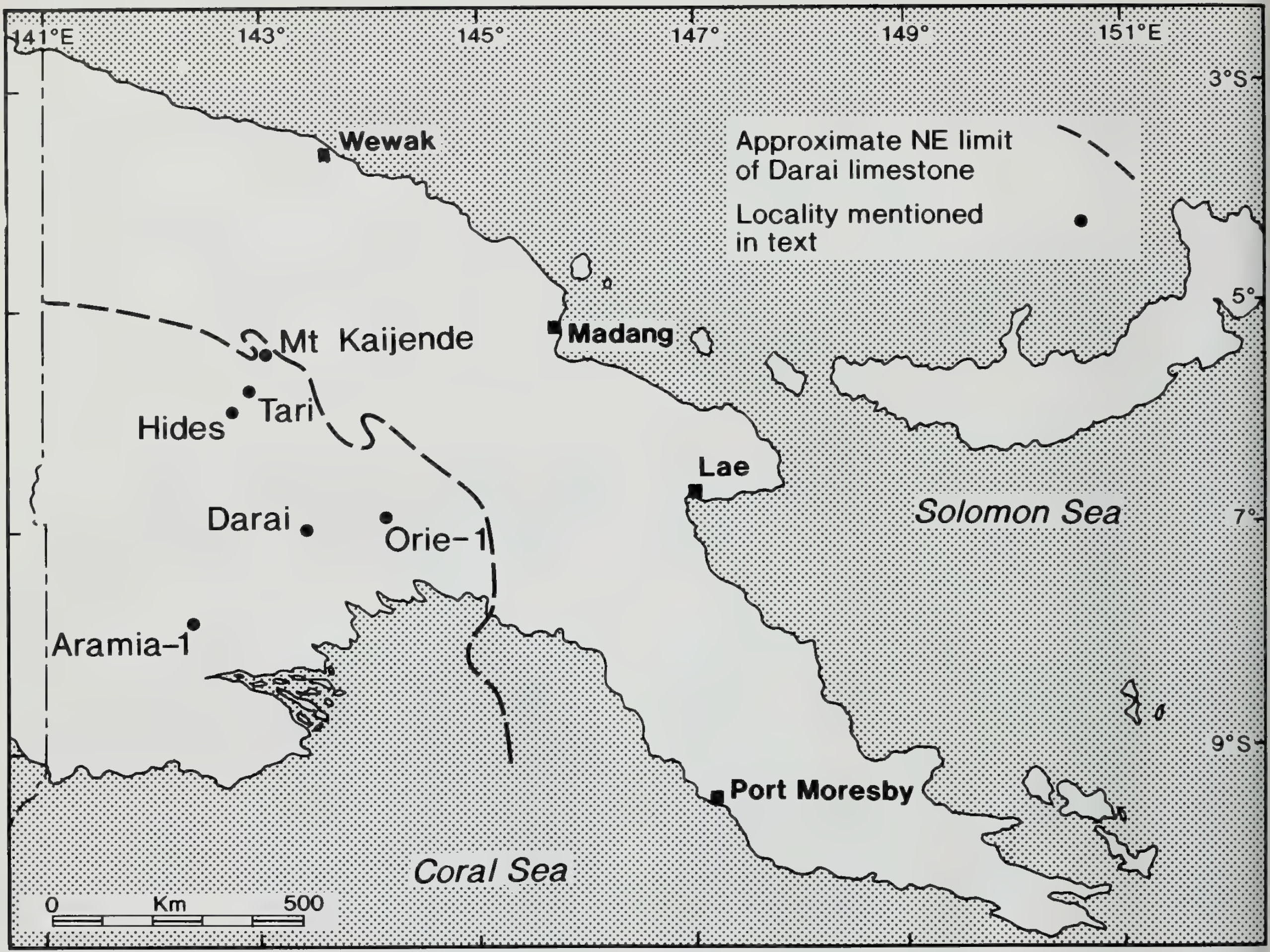


Fig. 1 Map showing the principal localities mentioned in the text.

members typically have spherical to fusiform tests. The recorded evolutionary history of the family is characterized by discontinuity, with periods of high diversity and morphological complexity alternating with poorly documented intervals of low diversity. The Cenomanian, the Senonian, and the Late Palaeocene to Mid Eocene are periods of abundance, whereas the Turonian, Maastrichtian, Early Palaeocene, and Late Eocene to Early Oligocene are characterized by low species diversity and relatively small numbers of individuals. These alternating periods of high and low diversity, and the apparent absence of morphotypes intermediate between genera in successive bloom periods, have led some authors to believe that the family could have originated several times from an obscure milioline stock and thus be polyphyletic. This was, indeed, implied by Reichel (1964), who noted that 'the Alveolinidae [is] a morphologically well-defined family but probably not a phylogenetic unit. Some of the genera that followed each other in the course of geological epochs surely did not evolve one from another.' Although Reichel (1964) did not imply that the genus *Alveolinella* contributed to the polyphyletic nature of the family as a whole, he certainly knew of no species transitional to its probable ancestral genus, *Flosculinella*.

Compared with the number of early Palaeogene species attributed to *Alveolina*, the three or four Neogene genera are poorly diversified. This, however, may reflect the relative paucity of suitable Neogene sedimentary environments (shallow-water carbonates were less widespread than in the Eocene) as much as any innate failure of the group as a whole to radiate.

In this paper, the transition from *Flosculinella* to *Alveolinella* is documented by the description of *A. praequoyi* n. sp.

SYSTEMATIC DESCRIPTION

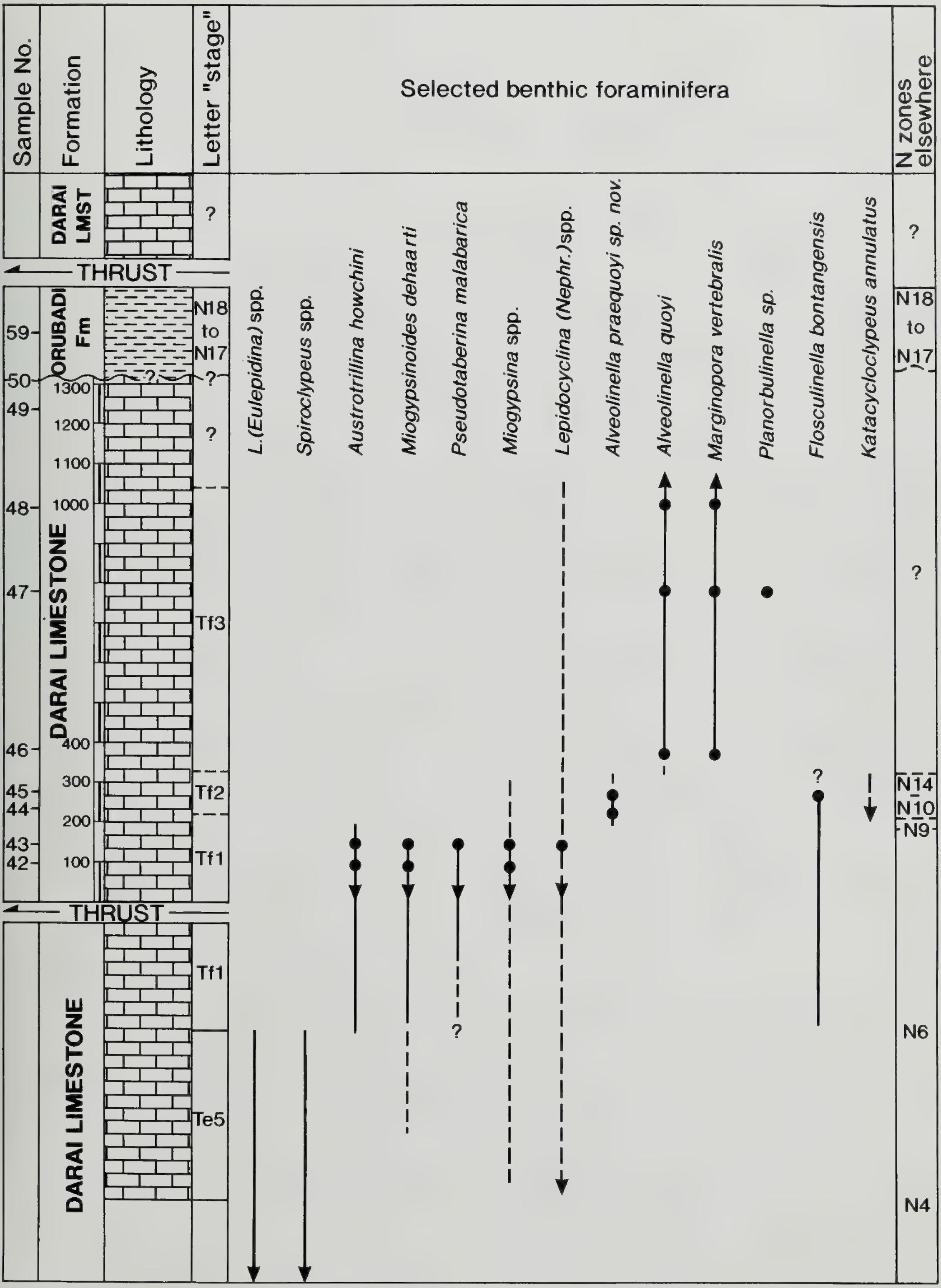
Order **FORAMINIFERIDA** Eichwald, 1830
Suborder **MILIOLINA** Delage & Hérouard, 1896
Superfamily **MILIOLACEA** Ehrenberg, 1839
Family **ALVEOLINIDAE** Ehrenberg, 1839

Genus ***ALVEOLINELLA*** Douvillé, 1906

TYPE SPECIES. *Alveolinella quoyi* (d'Orbigny, 1826).

Alveolinella praequoyi sp. nov. Figs 4–7

?1896 *Alveolina* sp. Verbeek & Fennema (pars): 1142; pl. 11, figs 43a, b only.



ig. 2 Composite stratigraphical section through the Miocene part of Hides Anticline sequence, Papua New Guinea, showing the ranges of important stratigraphical markers including *A. praequoyi* sp. nov. Broken lines indicate ranges elsewhere in the Darai Limestone; black spots mark sample levels. Only the measured part of the limestone is to scale.

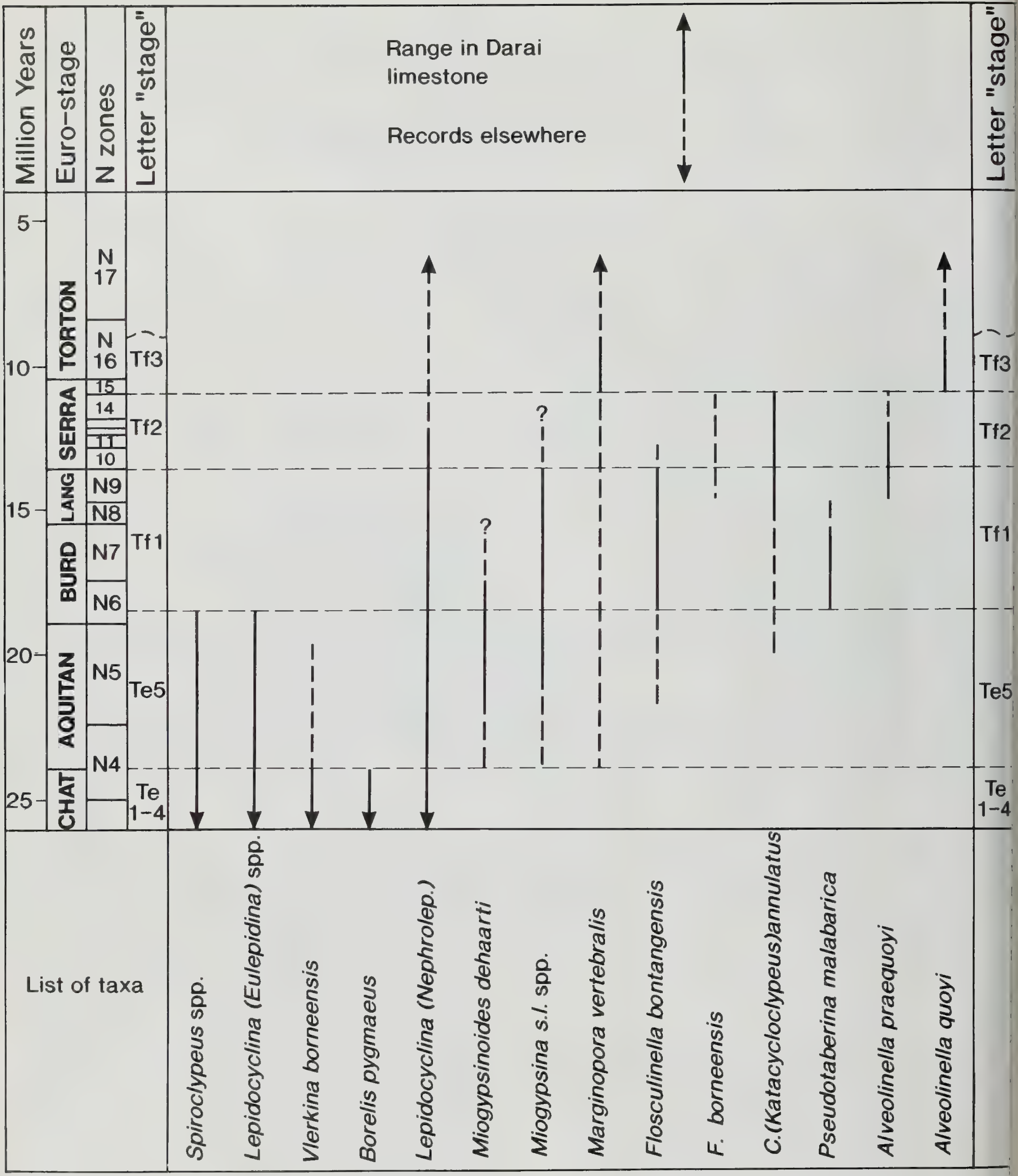


Fig. 3 Known ranges of some important Miocene larger foraminifera in Papua New Guinea and other parts of the Indo–West Pacific region. The smaller benthic marker genus, *Austrotrillina*, is not known above N9 (see Adams, 1984).

?1909 *Alveolina fennemai* Checchia-Rispoli: 67.
1962 *Alveolinella* sp. Eames *et al.*: pl. 6, fig. D.
?1973 *Alveolinella* sp. Binnekamp: 8.
1984 *Alveolinella fennemai* Checchia-Rispoli; Adams: 54, 59.

DIAGNOSIS. A fusiform alveolinid, initially *Flosculinella*-like (i.e., with an irregular juvenile coil and two rows of chambers per whorl in the later nepionic stage), followed by an *Alveolinella*-like adult stage comprising no more than 2–3 whorls.

NAME. To indicate that it is probably ancestral to d'Orbigny's species *A. quoyi*.

TYPE LEVEL. Early Middle Miocene (upper Tf_1 to Tf_2) part of the Darai Limestone.

TYPE LOCALITY. Unnamed river gorge. NE flank of Hides Anticline, Central Highlands, Papua New Guinea. Sample horizon 45, of B.P. Australia Ltd. Local grid reference 9119/4514.

MATERIAL. Numerous individuals seen in randomly orientated thin sections, plus 3 orientated thin sections from sample 45.

DESCRIPTION. Megalospheric form: test porcellanous, large, fusiform; initially streptospirally coiled, but becoming planispiral after the first 1–2 whorls. Chambers axially elongated, numerous; about 18 in the last whorl. Proloculus 0·06–0·08 mm in diameter (2 measured individuals). Two principal layers of chamberlets per whorl, the outer row (attics of authors) being smaller and twice as numerous as the inner. Both rows are present throughout the post-streptospiral stage of growth. Towards the poles, one or more additional rows of chamberlets appear in the last 3 or 4 whorls; these extend towards, and eventually cross, the equator in the adult stage. The extra rows are intercalated between the primary chambers and the attics, and accommodated by a thickening of the basal attic wall: these chamberlets are never more numerous than those in the primary rows. Septula continuous, at least in the adult stage. The preseptal passage is basal, and well-developed in the later ontogenetic stage, as in *A. quoyi*. Apertures not visible in random sections.

Microspheric form not definitely observed.

DIMENSIONS of holotype (P52658; Figs 5a, b): length 3·4 mm, width 1·03 mm. Whorls 7; the first is slightly eccentric. Maximum internal diameter of proloculus 0·08 mm.

REMARKS. *Alveolinella praequoyi* differs form all known species of *Flosculinella* in having more than two rows of secondary chamberlets in the later ontogenetic stage. It differs from Late Miocene to Recent representatives (Miocene forms are poorly known, but see Fig. 12) of *A. quoyi* in having a smaller proloculus (0·08 mm or less compared with 0·10–0·22 mm), an irregular initial coil and a distinct juvenile stage of several whorls with only primary chamberlets and attics. The third (and any subsequent) rows of secondary chamberlets are confined to the polar regions except in the last few whorls. Adult megalospheric individuals of *A. quoyi* are often twice as long as mature individuals of *A. praequoyi* (compare Figs 8 and 10 with Figs 4, 5a and 7).

It is possible that *A. fennemai* (Checchia-Rispoli) will eventually prove to be a senior synonym of *A. praequoyi*. However, we think it better to use the new name until *A. fennemai* can be adequately redescribed and refigured from topotypic material. It is just possible that Binnekamp's unillustrated record (1973) of *Alveolinella* sp. from the lower part of the Yalam Limestone, New Britain, should be referred to *A. praequoyi*.

ASSOCIATED FAUNA. This is restricted to *Elphidium* sp. indet., other smaller benthic species and soritids in the Tf_1 part of the type section. Elsewhere, e.g. in the Orie and Darai anticlines (samples 364KRA, 963KRA and 1056KDA, 77KF), and in other parts of the Tari area (samples 21KT and 22KT), *A. praequoyi* has been found with one or both of *A. howchini* and *F. bontangensis* in beds of Tf_1 age. Although it occurs within the range of *Katacycloclypeus annulatus* (Tf_2 in the Darai Limestone, but extending down into Tf_1 elsewhere), the two species have not yet been found in direct association, probably owing to palaeoenvironmental constraints. See Figs 2 and 3.

Belford (1984: 33) reported what now appears to be an anomalous association of *Miogypsina* (*M.*) sp., *Austrotrillina* sp., and *Alveolinella ?quoyi*, in Sample KJ10 from the Darai Limestone near the summit of Mount Kaijende (Fig. 1). We have been able to examine this material and can confirm the presence of a single, slightly off-centre, section of *Alveolinella*, which could be either a large *A. praequoyi* or a true *A. quoyi*. It occurs with *Austrotrillina* sp. indet., and an advanced, but specifically indeterminable, *Miogypsina*. The rock itself is a grainstone and contains small clasts of reworked *Globigerina* limestone. It is possible that much of the assemblage, particularly the specimens of *Austrotrillina* and *Miogypsina*, are reworked and that the age of this sample is Late Miocene or younger. If so, it cannot form part of the Darai Limestone proper. A similar assemblage has not been found in any of the hundreds of samples examined independently by us from this region. Unfortunately, no other samples were collected from the vicinity of KJ10, and the original sample is now missing (Dr G. C. H. Chaproniere. Canberra, personal communication).

STRATIGRAPHICAL DISTRIBUTION. Middle Miocene (latest Tf_1 through Tf_2 in terms of the East Indies Letter Classification).

GEOGRAPHICAL DISTRIBUTION. As yet known with certainty only from Papua New Guinea, but some poorly illustrated records of *A. fennemai*, *Alveolinella* sp., and, perhaps, *Flosculinella borneenis* (Tan) from the Indo-West Pacific region may be referable to this species.

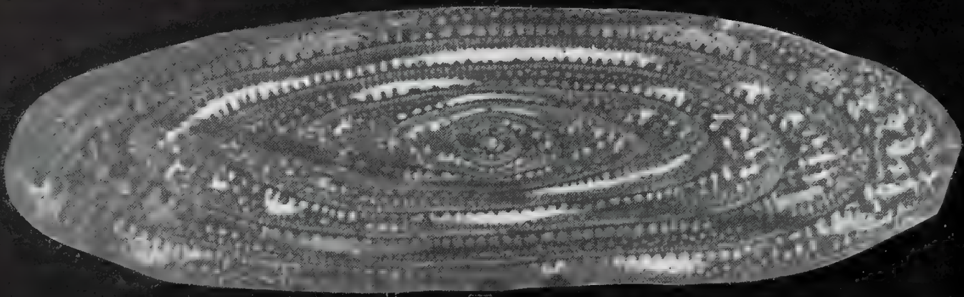
CHRONOSTRATIGRAPHIC SIGNIFICANCE. *Alveolinella praequoyi* first appears with *Austrotrillina howchini* in the upper Tf_1 part of the Darai Limestone (Sample 44 in our material) and persists locally throughout Tf_2, i.e., throughout the greater part of the Middle Miocene shallow-water carbonate sequence as developed in Papua New Guinea. Its short range suggests that it could become a valuable stratigraphical marker throughout the eastern part of the Indo-West Pacific region.

The *Alveolinella*-bearing limestones are developed in perireefal facies characterized by the taxa shown in Fig. 2.

DEVELOPMENT AND EVOLUTION

Since the discovery of *Flosculinella* by Schubert (1910), most authors, including Reichel who monographed the family in 1936–37, have regarded it as ancestral to *Alveolinella* despite the apparent absence of intermediate forms.

The possibility that *Alveolinella* arose from *Borelis*, a genus which appeared in Eocene times and lives on in tropical seas today, can certainly be discounted since the latter is characterized by the possession of a single row of chamberlets. Only *B. curdica* (Reichel) has shown a tendency to develop a second row, and in this species the chamberlets of the primary and secondary rows alternate in position and are therefore approximately equal in number. *Flosculinella* and *Alveolinella*, on the other hand, have two attic chamberlets for every one in the primary row.



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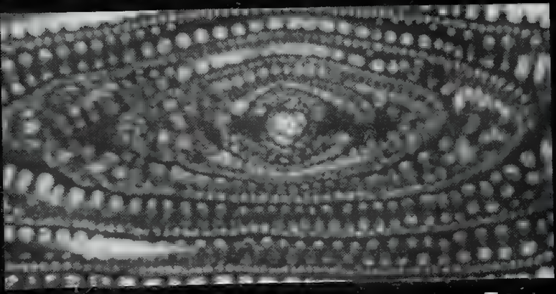

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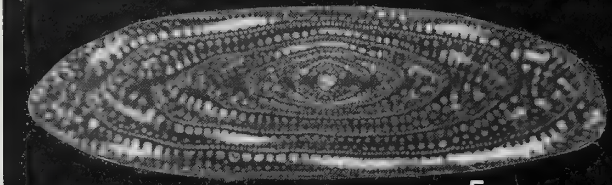

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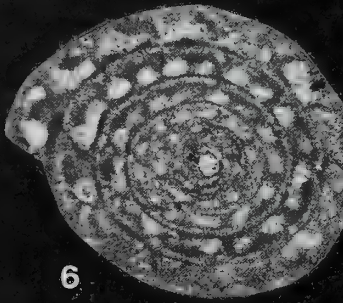

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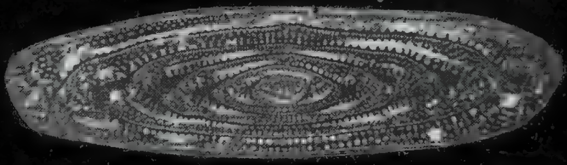

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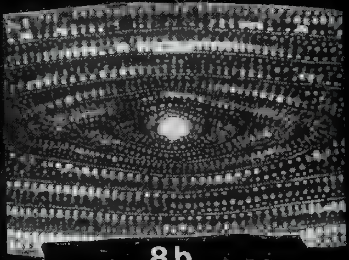

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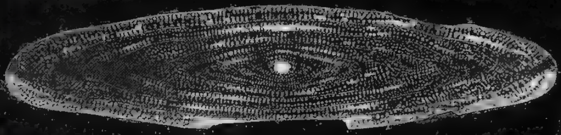

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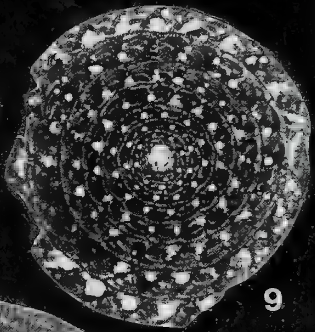

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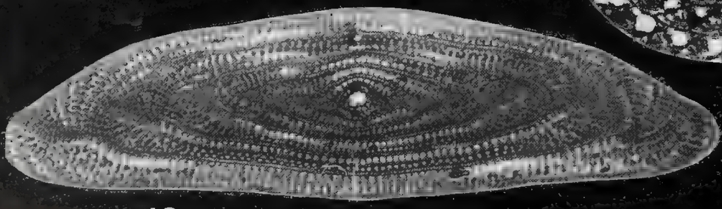

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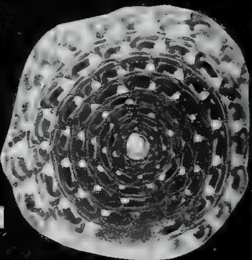

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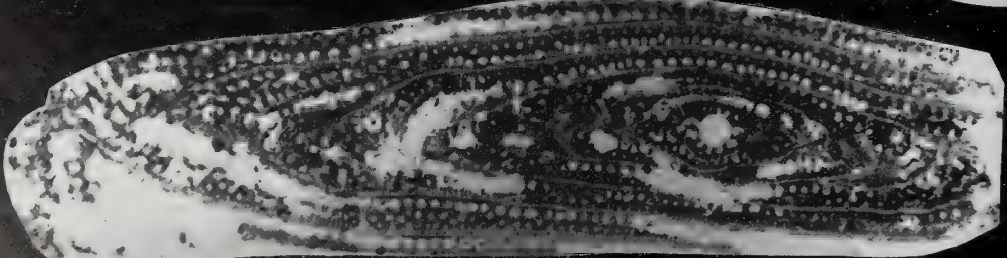

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Borelis is usually regarded as the probable ancestor of *Flosculinella*, although transitional forms have not yet been found.

The probable ancestor of *Alveolinella praequoyi* is *Flosculinella bontangensis*, a commonly occurring species in the Darai Limestone. It may well be that *F. bontangensis* grades into *F. borneensis* (from which it differs mainly in having a lower length/breadth ratio), and it would not, therefore, be surprising to find that the length/breadth ratio of *A. praequoyi* is rather variable, as seems to be suggested by the present material. For good illustrations of *F. borneensis* see Binnekamp (1973: pl. 2, figs 3–6). The only difficulty in deriving *Alveolinella* from *Flosculinella* lies in the fact that *Flosculinella* is said to possess septula which alternate in position between adjacent chambers whereas they are continuous in *Alveolinella* (Reichel 1936–37, 1964). The present material does not permit us to comment on the arrangement of septula in the juvenile stage of *A. praequoyi*.

One of us (Adams, 1983) suggested that the appearance of the attic row of chamberlets in *Flosculinella* was an example of the sudden evolutionary production of 'novelty' in the Foraminifera. This may well be true, but the introduction of the third row of chamberlets in *Alveolinella* is evidently a further example of gradualism.

ACKNOWLEDGEMENTS. We are grateful to Dr G. C. H. Chaproniere (Bureau of Mineral Resources, Geology and Geophysics, Canberra) for the loan of material from Papua New Guinea, and both to him and Dr. D. J. Belford (B.M.R.G.G., retired) for helpful correspondence regarding the Mount Kaijende sample. Dr Alan Lloyd (W. Australia) provided useful information on the faunas of the Darai Limestone, and Mr R. L. Hodgkinson (B.M.N.H.) prepared the orientated thin sections. This paper is published with permission kindly granted by B.P. Research International and B.P. Australia Ltd.

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Figs 4–7 *Alveolinella praequoyi* sp. nov. Fig. 4, from Australasian Petroleum Co. sample 77KF, Darai Hills, associated with *Austrotrillina howchini*; age Tf_1. × 33. Figs 5a, b, **holotype** P52658, equatorial section of megalospheric form; a × 24, b (centre of test) × 48. Note irregular initial coil and gradual development of the third layer of chamberlets (see also Fig. 4). Fig. 6, P.52659, transverse section, × 48. Fig. 7, P52660, random off-centre section, × 19. Figs 5–7 all from sample 45, Hides Anticline, Central Highlands, Papua New Guinea.

Figs 8–12 *Alveolinella quoyi* (d'Orbigny). Figs 8a, b, 9, Plio-Pleistocene specimens from the Togopi Formation, North Borneo; sample NB9452 (see Whittaker & Hodgkinson 1979, for details of provenance). Note kidney shape of proloculus and planispiral coil. Figs 8a, b, P52661; a × 9·5, b × 19. Fig. 9, P52662, × 24. Figs 10, 11, sections of Recent individuals for comparison with *A. praequoyi*. Fig. 10, ZF 4911, equatorial section, × 19; New Caledonia. The subspherical appearance of the proloculus is misleading; better-orientated sections of incomplete specimens show that it is kidney-shaped. Fig. 11, ZF 4912, transverse section, × 24; Maldive Islands. Fig. 12, from Australasian Petroleum Co. well Aramia-1, 886–896 m; age early Tf_3. × 33. Figured for comparison with Fig. 4. Proloculus shape may be misleading since the centre is unclear. Note the initial planispiral coil. Few, if any, previous figures exist of *Alveolinella* from beds of Tf_3 age.

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'Placopsilina' cenomana d'Orbigny from France and England and the type species of *Placopsilina* d'Orbigny, 1850 (Foraminiferida)

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Synopsis. English *Placopsilina* /*Lituola cenomana* specimens in the British Museum (Natural History) are closely similar morphologically to material collected from the Upper Cretaceous type area of Le Mans, France. The French material, however, has a randomly arranged, coarsely agglutinated solid wall structure, whereas the English specimens from the Chalk show a radial alignment of calcitic grains; the latter are therefore re-assigned to '*Placopsilina*' *northfleetensis* sp. nov. We at present depend for generic information on d'Orbigny's descriptions of *P. cenomana* and *cornueliana* d'Orbigny, although the poorly diagnosed species *scorpionis* is the type of *Placopsilina* d'Orbigny (1850*a*) by monotypy; Cushman (1920) was in error in designating *cenomana* d'Orbigny (1850*b*) as type. The name '*Placopsilina*' is therefore used in quotes.

INTRODUCTION

Housed in the Micropalaeontology section of the British Museum (Natural History), London are numerous specimens, presented by various collectors, of an adnate agglutinating foraminifer, labelled *Placopsilina* or *Lituola cenomana* d'Orbigny, from English Cretaceous localities. Their assignment to *cenomana* follows Carpenter *et al.* (1862: 143; pl. XI, figs 11–14), who no doubt considered their specimens conspecific with those described, but not figured, by d'Orbigny (1850*b*) from Le Mans, France. I have attempted to verify that the English material is the same as that from the type area of *cenomana*, and to address the possibility that *cenomana* is synonymous with *Placopsilina cornueliana*, described by d'Orbigny in the same paper. But the problem of generic placement has not been overcome (see below); all references here to the genus, other than to those by d'Orbigny, are thus in inverted commas.

Cushman's (1920) designation of *P. cenomana* d'Orbigny (1850*b*) as type species is incorrect. He was unaware, possibly because of the confusion over publication dates (Sherborn 1922), that *Placopsilina scorpionis* d'Orbigny (1850*a*) was the genotype, by monotypy. This species, to my knowledge, has never been properly investigated and because type material is unavailable cannot be investigated here. The diagnosis of the genus thus still depends upon the interpretation of the descriptions of *cenomana* and *cornueliana* by Reuss (1862), and also by Carpenter (1862). D'Orbigny paid no attention to wall composition, so it is possible that on investigation the wall of *scorpionis* will be found not to be agglutinating. In that case both *cenomana* and *cornueliana* as now interpreted would be referred to a new or existing genus other than *Placopsilina*, but any attempt to do so here is considered premature. Additionally, no syntypes of either *cenomana* or *cornueliana* have been found and the designation of neotypes from other material, because of the incompleteness of our knowledge, is inadvisable at present.

THE TAXONOMIC BACKGROUND

The first published reference to *Placopsilina* made by d'Orbigny was in the first volume of the *Prodrome* (1850*a*: 259), when he included it in his 9th stage, Toarcian, among the foraminifera:

'***PLACOPSILINA***, d'Orb., 1847. Ce sont des Wibbina [*sic*] à locules pleines.

***283. scorpionis**, Espèce très-rugueuse et très-diversement contournée. France, Saint-Maixent (Deux-Sèvres).' (The Département of Deux-Sèvres is in western France.)

No illustration was given. The date 1847 was the year in which d'Orbigny completed the manuscript of this first volume, but its expected publication date of 1848 was delayed by a revolution in that year, so that the printed version could not appear before 1849 (d'Orbigny 1850*a*: lxi; Heron-Allen 1917: 61). Some of the printed copies of the first volume did in fact bear the date 1849 on their title-pages, but it was not published until January 1850 (1850*a*) and the remaining copies were revised to bear the name of this new year; a copy was presented by d'Orbigny to the Societé Géologique de France, Paris, on January 21st 1850 (Sherborn 1922: xcviii).

In January, 1850, therefore, the genus *Placopsilina* was first published and it was monotypic, only the Toarcian species *P. scorpionis* being included. By ICZN (1985) Art. 68d, *P. scorpionis* must be the type species of the genus *Placopsilina* by original monotypy. The second volume of the *Prodrome* (1850*b*), containing *P. cenomana*, was not published until November 1850.

Cushman (1920: 70) subsequently designated *P. cenomana* as the type species of *Placopsilina*, during his studies on the Lituolidae. His selection of *P. cenomana* had not previously been seen to be erroneous probably because some of the copies of Vol. 1 of the *Prodrome*, as explained above, had their imprinted publication date revised to 1850, the same year as that imprinted on the title page of Vol. 2; the assumption was commonly (but erroneously) made that the two volumes had been published at the same time. In fact, the

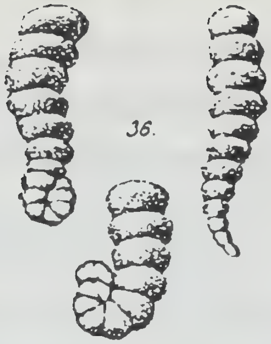


Fig. 1 *Placopsilina cornueliana* d'Orbigny 1850*b*. Reproduction of Cornuel's figure (1848: pl.2, fig. 36). Recorded in the plate explanation as 'Oeufs de Mollusques', the left hand illustration ('à gauche') was selected by d'Orbigny as the type figure of his new species; × 15.

second volume was not published until November 1850 (Sherborn 1922: xcviii). It is unfortunate that the name *cenomana* has been so widely cited while *scorpionis* remains virtually unknown.

In 1850*b* (November) d'Orbigny [p. 96], wrote of *Placopsilina*, 'Ce genre ressemble aux *Truncatulina*, mais est toujours fixe, et n'a d'ouverture qu'à la partie supérieure de la dernière loge'. Finally in 1852 [p. 119], he emended the diagnosis further, writing . . . 'C'est une *Truncatulina,* tout à fait fixée par la coquille, souvent projectée en crosse, dont l'ouverture occupe seulement la dernière loge'. Between 1850 and 1852 he erected the species *scorpionis*, *neocomiensis*, *cenomana* and *cornueliana* and placed them within *Placopsilina*, but only *cenomana*, to which our English specimens have been referred, and *cornueliana* are of concern here.

D'Orbigny (1850*b*) introduced the name *cornueliana* (No. 791) for a species from Vassy, which he considered synonymous with a specimen figured by Cornuel (1848: pl. 2, fig. 36, the left hand figure only) from Saint-Dizier (Haute Marne, north-east France), and referred to by the latter as 'Oeufs de Mollusques' (reproduced here, Fig. 1). This is the first illustration of a *Placopsilina*, but there was no accompanying description by Cornuel, except a mention of its size.

In 1862, both Reuss and Carpenter *et al.* independently added further interpretations to the diagnosis of the genus. Reuss (1862: 383) placed *Placopsilina* under *Nubecularia* Defrance (within the Lituolidea), thus implying that he considered d'Orbigny's genus to be a member of his group 'mit Sandig-Kieseliger schale'. Carpenter (1862: 143; pl. 11, figs 11–14) considered that *Placopsilina* (typified by *P. cenomana*) should be placed within 'Genus ***H.—LITUOLA***' . . . as having a 'test composed of an aggregation of particles obtained from external sources, the organic cement by which these particles are united being all that is furnished by the animal' (1862: 140).

Rhumbler (1913) placed *Placopsilina* in his new subfamily, the Placopsilininae. This was raised to family level by Cushman (1927: 41), who diagnosed it as having 'chambers simple, not labyrinthic'. This suprageneric assignment was retained by Loeblich & Tappan (1964, 1988), who defined the subfamily thus: 'Test attached; early stage coiled or arcuate, later uncoiled; wall agglutinated, solid'.

As recognition of the true identity of the type species, *P. scorpionis*, is beyond the scope of this paper, and, as I shall show, the definition of *Placopsilina* in terms of the wall structure needs further investigation, the generic assignment of my material is given as '*Placopsilina*' throughout the ensuing text to indicate that a thorough revision of the genus is very necessary.

THE FRENCH SPECIES

As we have seen, d'Orbigny erected in January 1850 (1850*a*) the new genus *Placopsilina* and a single new species (*P. scorpionis*) which, by monotypy, must be the type species, although the description, given above, was unsupported by illustration. The syntypes, which were his own specimens (marked *, see description, p. 1) have not been found in the d'Orbigny Collection in Paris (Vénec-Peyré, personal communication). No neotype has been designated, since the determinations supplied by Terquem (1866) of non-topotypic specimens from the Upper Lias of either the Départements de la Côte d'Or (eastern France) or de l'Indre (west-central France) have yet to be verified as conspecific (see original page in the Ellis & Messina *Catalogue of Foraminifera*, 1940). Until such time as Terquem's topotypes are found, or a neotype is designated, the true nature of *Placopsilina* will not be known.

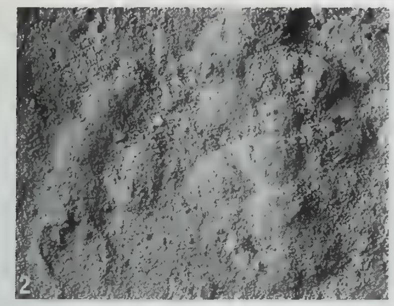
D'Orbigny erected two new species in November 1850 (1850*b*), *Placopsilina cornueliana* and *P. cenomana*.

Of *Placopsilina cornueliana* d'Orbigny (1850*b*: 111) no description was given, but it does not exceed 2 mm in length. The species was thought to be conspecific with the 'Oeufs de mollusques' mentioned and figured by Cornuel (1848: 259;

Figs 2, 5–8, 10, 13, 15 '*Placopsilina*' *cenomana* d'Orbigny. Examples of specimens from three localities in the Le Mans area (Sarthe), France. (For localities, see section on material studied, p. 4). Figs 2, 5–7, 10, 13, loc. 1. Fig. 2, P52773, poorly preserved specimens showing both crosier and nodosarid early chamber arrangement, × 30. Fig. 5, P52774, immature truncatuline forms, × 15. Fig. 6, P52776, portion of a fractured wall from specimen illustrated in Fig. 7, containing large randomly arranged angular grains, × 400. Fig. 7, P52776, illustrating meandriform method of growth and empty chambers, × 20. Fig. 8, P52777 (loc. 3), partially overgrown with bryozoa, × 20. Fig. 10, P52775, with well preserved truncatuline coil, × 13. Fig. 13, an intercameral aperture (specimen illustrated not identified). Fig. 15, P52778 (loc. 2), coarsely agglutinated form with crosier-shaped initial stage, × 27.

Figs 3–4, 9, 11–12, 14 '*Placopsilina*' *northfleetensis* sp. nov. Examples of English specimens attached to echinoid fragments from loc. 4 (see p. 4). Fig. 3, P40816(2), portion of a fractured wall from specimen illustrated in Fig. 4, showing radial arrangement of calcitic microgranules, × 600. Fig. 4, P40816(2), incomplete specimen following contour of substratum (see Fig. 3), × 41. Fig. 9, Paratype P40852(2) (see also Fig. 24), × 30. Fig. 11, P40818, showing the empty chambers, × 25. Figs 12, 14, **Holotype** P40852(1) (see also Fig. 32), Fig. 12 showing initial coil, followed by crosier and later rectilinear growth; note also position of the terminal basal aperture, × 23; Fig. 14 close-up of intercameral aperture, × 60.

Scanning electron micrographs. Figs 2, 5, 8–12, 14 are uncoated and were studied using back scattered electrons in an environmental chamber. (The scanning electron microscopes used were the ISI 60A and ISI ABT 55 models).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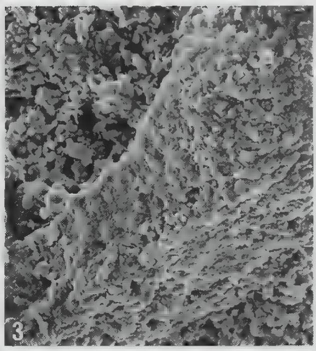
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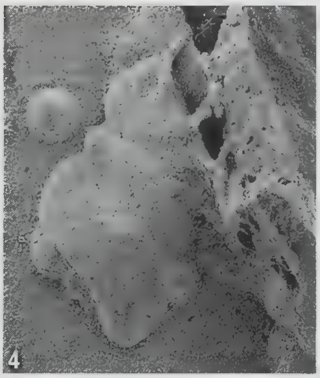
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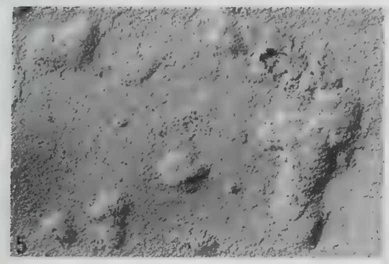
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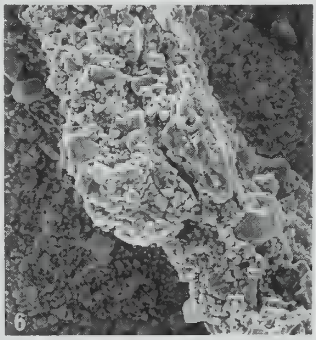
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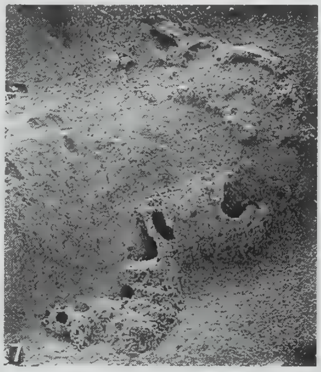
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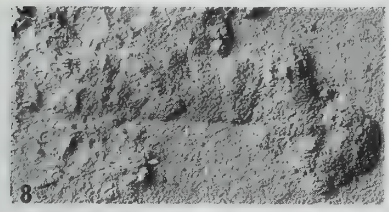
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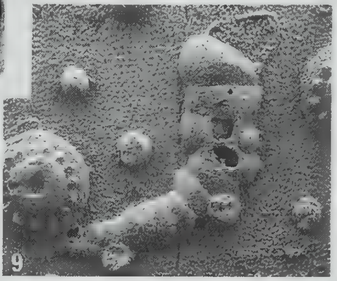
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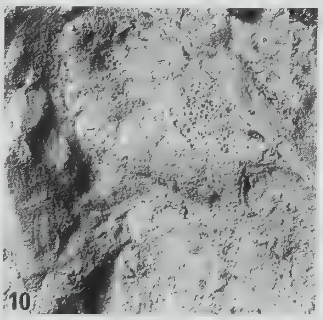
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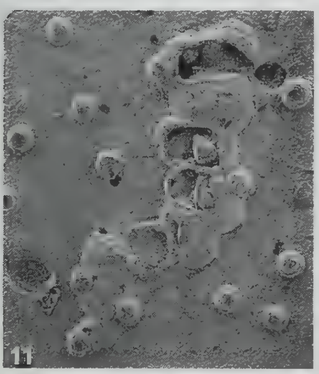
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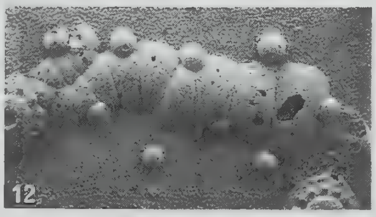
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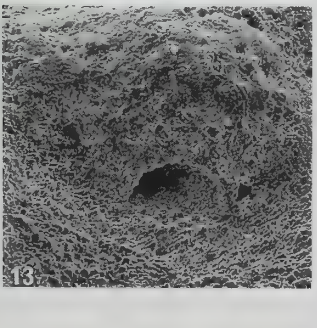
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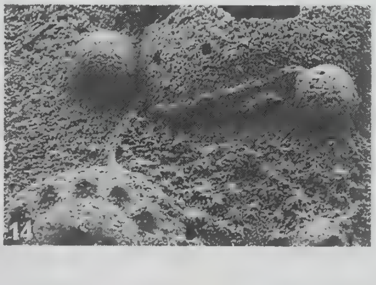
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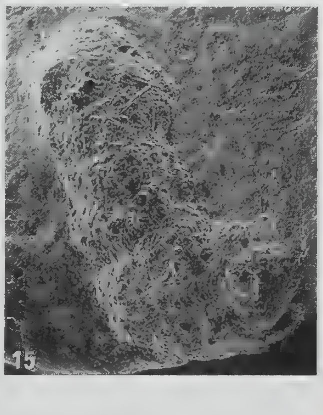
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pl. 2, fig. 36, the left hand figure only), and here reproduced as Fig. 1. It was recorded as occurring in the 17e Étage : Neocomien, marne calcaire bleue, at Saint Dizier. In a personal communication, Marc Barbier, the Saint Dizier Museum curator, expressed a hope that when curation was completed, these specimens might be found.

Placopsilina cenomana d'Orbigny (1850*b*: 185) was described merely as an 'Espèce contournée en crosse adhérente aux corps'; it was not figured. It was recorded from the 20e Étage : Cenomanien, at Le Mans (Sarthe). D'Orbigny indicated by a * that the specimen was his own (1850*a*: lv), which leads me to assume that it may still be present, unrecognized, somewhere within a d'Orbigny collection, although it cannot be found in the Muséum National d'Histoire Naturelle, Paris (Vénec Peyré, personal communication). It is unwise therefore to designate a neotype.

Although the failure, at present, to find syntypes of either of the above species hampers proper taxonomy, by using known facts it is possible to build up a picture of a genus and species which, when applied to material from the type area, can provide significant information. First, from Cornuel's figure, the shape, size and form of '*Placopsilina*' can be deduced. Secondly, for *cenomana* there is a brief description (see above). A broad picture of '*Placopsilina*' can thus be drawn from d'Orbigny's descriptions.

It can be *Truncatulina*-like in shape, or with a coil of many chambers sometimes laid down in a crosier-like configuration and extended in a rectilinear manner, all parts being fixed to the substrate with an aperture on the superior part of the last chamber. The length is up to 2 mm.

About the wall structure there is no information, however. D'Orbigny observed that *Placopsilina* was '*Wibbina*-like' in form. (Probably he meant *Webbina*-like, for I cannot find the term *Wibbina* used in any context). Although the fixed inequilateral form of these two genera was similar (see Le Calvez, 1974, for information on *Webbina rugosa*, the type species of *Webbina*) there must have been some fundamental difference observed by him in separating them. I can only speculate that the placopsilinids were more truncatuline, rather than nodosarid, in form in some specimens, and that the composition of the test was unusual; the latter, however, d'Orbigny did not consider important. Reuss (1862) and Carpenter (1862) were left to speculate on its agglutinating nature, since there is no indication that either had any contact with d'Orbigny and there is no information from publications that they saw d'Orbigny's specimens.

THE PRESENT MATERIAL

The French material. Because syntypes are not available and localities given by d'Orbigny are not of the accuracy required by modern collectors, only an examination of material from the same stratigraphic age in the vicinity of the type locality, present in the extensive collections of the British Museum (Natural History), London, could be undertaken.

Saint Dizier. The type locality of '*P.*' *cornueliana*. No placopsilinids were found, although brachiopod shells from this locality (in the care of C.H.C. Brunton), in particular, were carefully examined.

Le Mans (Sarthe). The type locality of '*P.*' *cenomana*. This material was more abundant, numerous molluscs having been collected by P.D. Taylor and J. Hammond in 1985 from Le Gasonfier 1 (Middle Cenomanian, Sables de Mans) [**Locality No. 2**] and 2 (Upper Cenomanian, Sables du Perche) [**Locality No. 3**]; also from the Lower Cenomanian *Mantelliceras saxbii–Hysteroceras orbignyi* Zones, Sables et Grès de Lamnay (lumachelle), Lamnay, Sarthe [**Locality No. 1**] for the study of bryozoa. Only a very small proportion of the shells carried adnate, agglutinating foraminifera and it is mostly on these specimens that the following work is based. Other specimens were found in the *Girvillella* shell bed, 3 m below proven Lower Cenomanian, in a roadside bank alongside route N831, D6, 200–300 m north of the church at St Mars, S. Ballon, Sarthe, France (W.J. Kennedy Collection).

The English material. This was predominantly obtained from the A.W. Rowe Collection, from the Santonian *Micraster coranguinum* Zone at Northfleet [**Locality No. 4**] and Margate, Kent (P40805–25 and 40827–61), over 60 specimens being examined.

Additional specimens from the W.B. Carpenter Collection, housed in the Royal Albert Memorial Museum, Exeter (their Catalogue number 263/1903.816) were also studied. Specimens figured by Carpenter (1862: pl. 11, figs 11, 12 and 14) were recognized and are re-figured here as Figs 16, 20 and 21. It is unfortunate that none of these specimens is localized, being simply labelled 'Chalk'. Twelve attached specimens were measured; the remaining nine are unattached and ignored for this study. No apertures were observed, but the dimensions of the specimens tend to exceed the examples from the Rowe Collection.

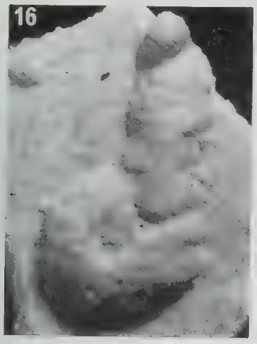
Additional material in the BM(NH) collection, which has

Figs 16–27, 32–34 '*Placopsilina*' *northfleetensis* sp. nov. Figs 16–21 from the Chalk (of England); the register number of all (263/1903.816) is that of the Royal Albert Memorial Museum, Exeter. Figs 16, 20, 21 were drawn by Carpenter *et al.* (1862) and are re-illustrated here. Fig. 16 (Carpenter 1862: pl. 11, fig. 12), × 14. Fig. 17, magnification not known. fig. 18, × 25. Fig. 19, × 22. Fig. 20 (Carpenter 1862: pl. 11, fig. 14), × 11. Fig. 21 (Carpenter 1862: pl. 11, fig. 11), × 12. Figs 22–27, 32–34, loc. 4 (see p. 4). Fig. 22, P40809(1), overcrowding of specimens around pores in echinoid shell, × 5. Fig. 23, P40814, overcrowding has masked the true form of the specimens (note the long rectilinear portions in these forms as well as that illustrated on Fig. 34), × 5. Fig. 24, Paratype P40852(2) (see also Fig. 9), × 25. Fig. 25, P40835(4), specimen sculptured around the spine bosses of an echinoid (note the empty chambers and apparent lack of a basal wall), × 20. Fig. 26, P40835(2), × 30. Fig. 27, P40835(3), × 18. Fig. 32, **Holotype** P40852(1) (see also Figs 12, 14), × 20. Fig. 33, P40822, natural weathering has opened the rectilinear portion showing the empty chambers, × 10. Fig. 34, P40813 (see also Fig. 23), × 4.

Figs 28–30, 35 '*Placopsilina*' *cenomana* d'Orbigny. French specimens from the Le Mans area, Sarthe; for localities see p. 4. Fig. 28, P52779 (loc. 2), showing early truncatuline coil, × 30. Fig. 29, (loc. 2; this specimen lost during later development of the material), showing the crosier-like arrangement of earlier chambers (magnification unknown). Fig. 30, P52780 (loc. 3), initial coil followed by meandriform rectilinear chamber arrangement, × 22. Fig. 35, P52781 (loc. 1), specimen fitting closely to the contours of the shell on which it grew, × 18.

Figs 31, 36–37 Examples of '*Placopsilina*' from the Lower Cretaceous of southern England which have incorporated large grains into their tests. Fig. 31, P38030 (loc. 5), × 15. Fig. 36, P38037 (loc. 5), × 13. Fig. 37, P37917 (loc. 6), curving around a shell this specimen cannot be shown in its entirety, × 5.

All light photographs.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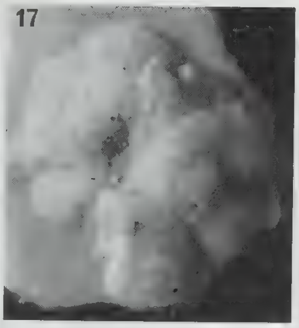
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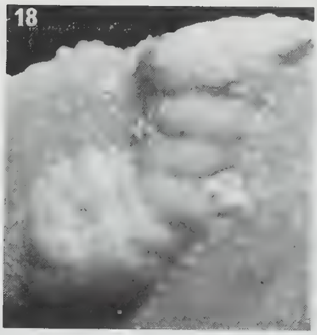
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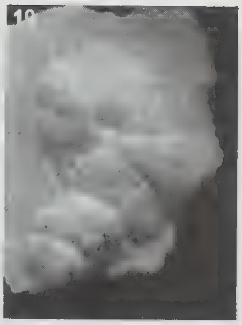
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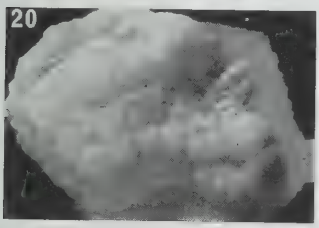
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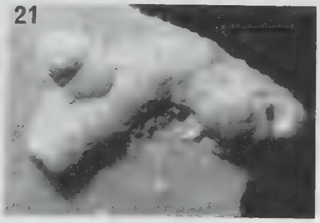
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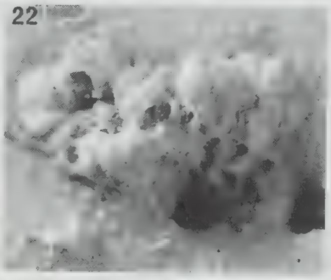
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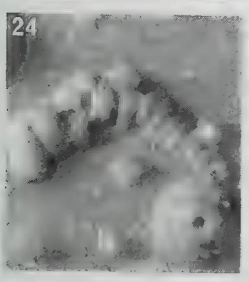
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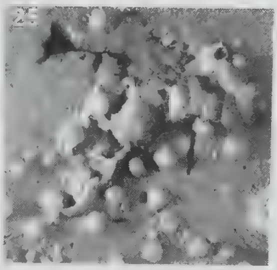
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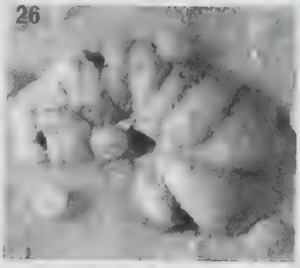
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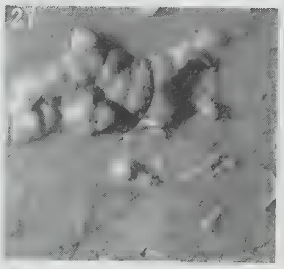
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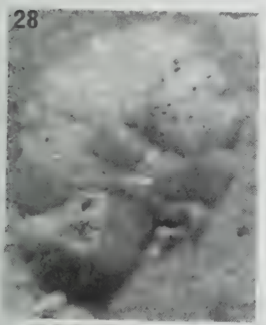
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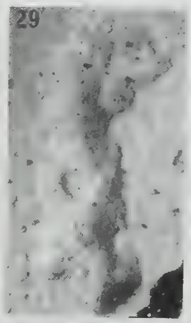
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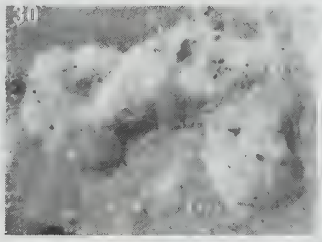
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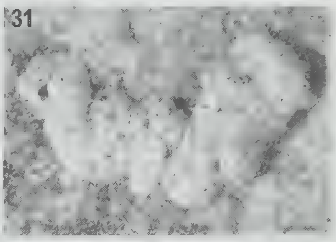
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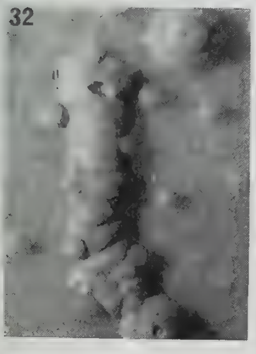
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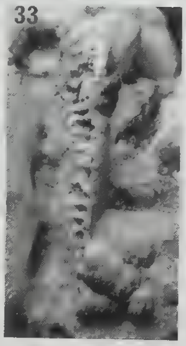
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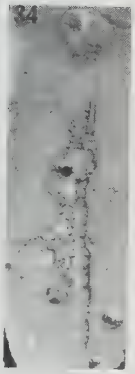
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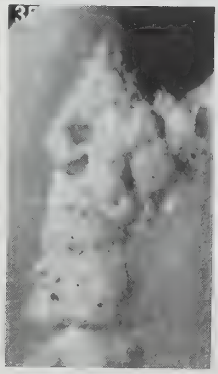
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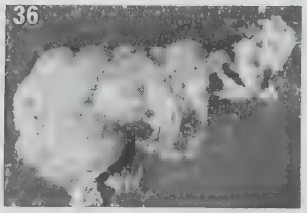
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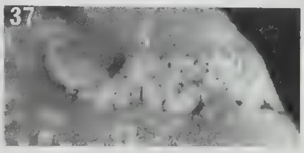
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been assigned to *cenomana*, is from the Aptian, Lower Greensand, Faringdon beds, Little Coxwell Pit at Faringdon, Berkshire [**Locality No. 6**] (A.G. Davis Collection); and Lower Greensand sponge gravel, yellow gravel beds, Windmill pit at Faringdon [**Locality No. 5**] (T.F. Grimsdale collection). Also from the Albian, Gault of Zone XI, at Folkestone (Chapman Collection); the Red Chalk of Hunstanton (G.R. Vine Collection); and the Santonian *Uintacrinus socialis* Band at Margate and possible specimens from the Campanian *Belemnitella mucronata* Zone (both A.W. Rowe Collection). These additional examples are not discussed in detail here since they will form part of a general review of agglutinating, adnate forms under preparation by others. They are mentioned here to illustrate that the 'genus' was present in the area now represented by southern England from Aptian to Campanian times.

Although comparison between typical English and French specimens is relatively easy, there are many English forms from the Chalk which have lost symmetry, intergrown and developed long rectilinear portions (Figs 23, 34). One English specimen from the Aptian at the Windmill Pit, Berkshire (P38038) is very large (8·6 mm long with large included grains). The configurations of the test, as illustrated in my figures, is one of great irregularity, and it is noteworthy that the majority of English specimens, especially those from the Chalk, are composed of very fine-grained material.

NEW INFORMATION ON FRENCH AND ENGLISH MATERIAL

Dimensions

FRENCH specimens		ENGLISH specimens
11	Number of specimens measured	20
3–7+	Number of chambers in coil	5–8+
2–7	Number of rectilinear chambers	8–13
0·9–2·90 mm	Length of test	1·85–2·90 mm
0·5–0·95 mm	Coil width	0·15–0·48 mm
0·05–1·4 mm	Coil length	up to 1 mm
0·3–1·0 mm	Width of rectilinear portion	0·45–0·9 mm
0·15–0·35 mm	Chamber height rectilinear portion	0·2–0·40 mm

Wall structure. This was examined in both the French and English material by scanning electron microscopy of fractured surfaces and by routine sectioning and light microscopy. A basal wall was seen in all sectioned pieces, but whether it persists throughout growth of the rectilinear portion is uncertain (Fig. 25). In a thin section of a single English specimen (P52782, Fig. 38) thereappeared to be projections from the basal wall beneath the coil into the echinoid shell on which it lived, which could constitute some form of attachment for the newly settled specimen. Further study revealed differences in the wall composition and arrangement. Because relatively few specimens were available from Le Mans my investigations are not as complete as I would have liked. Nevertheless it is apparent that the wall of the French specimens appears to be irregularly constructed of large angular grains, cemented together (Fig. 6). Being adnate and surrounded by angular Precambrian debris (Juignet 1968) this would seem to be an obvious if not obligatory building material, whilst those from England have a wall composed of what appears to be calcitic microgranules cemented in a radially orientated pattern (Fig. 3) which has included much finer material derived from the Chalk sea. Coccoliths are in evidence, but it is possible that much of the wall was secreted by the animal. The radially orientated arrangement may be analogous to the canaliculi reported in the Haddoniidae (Chapman 1898), but in my opinion the wall of the English specimens is solid. Even if the size of the grains is environmentally controlled, the differences in their arrangement could be significant. These observations on the wall composition and arrangement cast doubt on the conspecificity of the French '*Placopsilina*' *cenomana* with the English specimens so named in our collections. For the moment, therefore, the English specimens are considered a new species (here named *northfleetensis*, opposite), until further evidence becomes available.

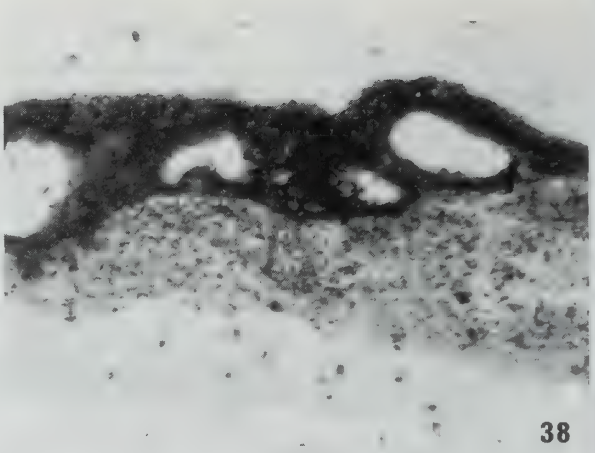
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Fig. 38 '*Placopsilina*' *northfleetensis* sp. nov. Light photograph of a thin-sectioned specimen from loc. 4 (see p. 4), showing projections from the basal wall beneath the initial coil into the echinoid shell on which it grew; P52782, × 120.

General Remarks. It is difficult to know which characters to choose when proposing a diagnosis of a new species or subspecies, especially since d'Orbigny's specimens of *cenomana* have not been examined recently. Both the French and English specimens have features in common: a basally attached crosier-shaped initial portion composed of simple, undivided chambers, followed by a basally attached rectilinear series of similar chambers which may use the substratum as a basal wall; the intercameral foramen is normally basal and terminal, lipped and semilunar in shape.

The difference between them lies in the composition of the test. It is being increasingly suggested that these differences in the formation of the wall are of importance taxonomically even at suprageneric level; nevertheless our lack of knowledge, as summed up by Hemleben & Kaminski (1990) underlines the need for caution here. Perhaps these species are 'programmed' to construct a framework of secreted calcite, and if in the environment there are large grains, they are collected and the secreted calcite changes form to mortar in the gaps. On the other hand, in environments where less detritus is available the secreted calcite framework continues to build, while the foraminifer collects what debris *is* available. If large grains are used, with plenty of secreted mortar specimens can grow to over 1 cm in size, it being easy for them to form chambers quickly, as demonstrated by attached specimens in our collections of an unidentified agglutinated species (P38030, Fig. 31; P38037, Fig. 36), from the Aptian

Faringdon Sponge Gravels. The smaller the grains available, and the greater the amount of secreted calcite mortar needed to hold them together, possibly mean in turn a higher level of test building intensity and the production of a porous framework to lessen the secretory process. Thus specimens using some large grains do less work and require less scaffolding to build their tests than those living in environments surrounded by only fine clastic material. Chemical examination with dilute hydrochloric acid appears to show that the French specimens cement their particles with calcium carbonate, but in fossil material such as this it would be difficult to estimate the amount of organic 'glycoprotein' cement, even if it were preserved as silica.

The young specimen cannot choose the substrate on which to settle and it may come to rest on coarse lag deposits or on a conglomerate (Sturrock & Murray 1981). It must use its pseudopodial net to obtain food and grains for shell building. As a placopsilinid is permanently attached and cannot browse, it must spread its net widely or somehow emplace itself in a depression on a living shell where food and moving particles would be most abundant. If attached to a shell, this would provide stability and, if the host animal was still alive, a means of mobility.

SYSTEMATIC DESCRIPTION

'Placopsilina' northfleetensis sp. nov.

Figs 3–4, 9, 11–12, 14, 16–27, 32–34

NAME. From Northfleet, Kent, England.

DIAGNOSIS. An initially coiled, later rectilinear, multichambered agglutinating test, composed of radially aligned calcitic granules.

HOLOTYPE. P40852(1), on an echinoid shell from the Santonian (*Micraster coranguinum* Zone), Northfleet, Kent, England (Figs 12, 14, 32). F.W. Rowe Collection. The paratype P40852(2) accompanies the holotype on the same piece of shell (Figs 9, 24).

OTHER SPECIMENS (on registered echinoid fragments): P40809, P40814, P40816, P40818, P40822, P40835.

DEPOSITORY. All material in Micropalaeontology (Foraminifera) Section, British Museum (Natural History), London.

DESCRIPTION (holotype). Test multichambered, agglutinating, attached throughout its entire length so that the attached surface is flat and the non-attached side convex. Chambers undivided and arranged in a linear manner, increasing regularly in height and width, the final chamber being the largest. There is a small, worn, initial coil (probably planispiral) followed by a crosier-like arrangement of chambers, later straightening into a final rectilinear portion of the test. Wall composed of calcitic microgranules cemented together and radially arranged.

Aperture: the last-formed chamber has been broken away, but the apertural imprint is terminal, basal against the substratum on which the animal was living. The intercameral aperture on the penultimate chamber is also basal, an arched slit across the central portion of the face, with an overhanging lip.

Dimensions: 19 chambers can be counted. Width of final chamber 0·61 mm; height of final chamber 0·35 mm; width of intercameral aperture 0·15 mm; diameter of coil 0·19 mm; length and width of 'crosier' 0·35 mm and 0·45 mm, respectively.

REMARKS. In spite of its morphological diversity, one specimen is selected as holotype to represent the species, but only for stability of nomenclature. Even the paratype on the same fragment (P40852(2), Fig. 24) shows variation. The specimens illustrated (Figs 16–23, 25–27, 32–34, 38), and those mentioned on p. 4 under 'English material', are not paratypes, since they are not on the same piece of echinoid shell as the type. They show many, but not all, of the forms this taxon may assume, given that they were seldom subject to overcrowding on the echinoid shells on which they are often found. As a result, many English specimens have lost symmetry, intergrown and developed long rectilinear portions, and it is not possible, in the majority of these cases, to recognize individuals. The wall structure, as revealed by scanning electron microscopy of fractured surfaces, is of calcitic microgranules cemented predominantly in radial, interconnecting rows. Without sectioning Carpenter's specimens (Figs 16–21) there is no certainty that they are conspecific, but it is assumed that they are.

A basal wall is present in all sectioned pieces of specimen, but may be absent in the later rectilinear portion. The dimensions of all measured English specimens are given earlier (p. 4) for comparison with my French material, thought to be *'Placopsilina' cenomana*, *sensu stricto*, from which *northfleetensis* differs in having a somewhat ordered arrangement of agglutinating material in the wall.

Examination of *Haddonia* Chapman (1898), the only other genus to which these specimens could, at present, be assigned, reveals that the wall contains coarse pores and the intercameral aperture is more an areal median slit with a tooth-like projection.

CONCLUSION

This investigation has revealed that Cushman (1920) was in error in designating *cenomana* as type of *Placopsilina*, because *P. scorpionis* d'Orbigny (1850*a*) was already type species by monotypy. Until a neotype is chosen for the little-known *scorpionis*, a task beyond the scope of the present paper, all other species referred by d'Orbigny (1850*b*, 1852) to *Placopsilina* should be cited in inverted commas. Should *scorpionis* prove to be the sole true representative of the genus *Placopsilina*, a reappraisal of all generic placements would have to be undertaken.

Initially I set out to answer two questions: first, can the English specimens in the British Museum (Natural History), identified as *Placopsilina* or *Lituola cenomana*, be equated with those of d'Orbigny? This question cannot be truthfully answered as I have not been able to locate d'Orbigny's type material, but it is unlikely now, with most major collections properly curated, that they will ever be discovered. If, however, the comparison is made using material collected in or near the type locality, and which can be interpreted as falling within the concept of d'Orbigny's species *cenomana*, then the latter is externally very similar to the English Santonian (*M. coranguinum* Zone) specimens from Rowe's collection and others mentioned above, at least superficially.

However, when the walls of English specimens revealed by fracture are examined under the scanning electron microscope, they are seen to differ significantly in structure and agglutination. For this reason the English specimens are here described as a new species. Since adnate, agglutinating species are at present under critical investigation by others (M. Simmons, personal communication), it is not considered appropriate here either to place them in a new genus or to include them within *Haddonia*, whose type species, the Recent *H. torresiensis* Chapman (1898, holotype BMNH no. 1897.11.20.1), has a very coarsely perforate wall and a different aperture.

The second question was, are *cenomana* and *cornueliana* synonymous? Even though *cornueliana* is from stratigraphically older beds there is no reason, at present, to suspect that it is any different from *cenomana*. D'Orbigny was a creationist: Heron-Allen (1917: 17) translates him as believing that, should he find 'in Nature forms, which after the most scrupulous analysis, present no appreciable difference, though they are separated by an interval of a few strata . . . I should not hesitate for an instant in regarding them as distinct'. Should the types of *P. cornueliana* ultimately be found in the Saint Dizier Museum or elsewhere (see p. 2), then that would be the time to make a formal statement on the synonymy (or otherwise) of the two species.

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A revision of the Middle Devonian uncinulid brachiopod genus *Beckmannia* Mohanti, 1972, and its distribution.

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SYNOPSIS. The Middle Devonian uncinulid brachiopod from Burma previously identified as *Markitoechia*? cf. *pentagona* (Kayser, 1871) is revised and assigned to *Beckmannia* Mohanti, 1972, and the new species *B. padaukpinensis*. A Givetian age for *Beckmannia* is favoured. This genus shows biogeographical affinities with the Rhenish–Bohemian Region of the Old World Realm and particularly of the Rhenish faunal province that extended into Burma and China.

INTRODUCTION

Anderson *et al.* (1969) described a rich collection of brachiopods from the Padaukpin limestones, in the Northern Shan States of Burma, as Eifelian in age. While examining this collection at the British Museum (Natural History) (BB 55500–89), we found that an uncinulid brachiopod described and figured (1969: 139-40; pl. 6, figs 1-4; text–fig. 4) as *Markitoechia*? cf. *pentagona* (Kayser, 1871) was in need of revision. This note deals with the taxonomic revision and comments on the stratigraphical and palaeo-biogeographical distributions of the uncinulid genus *Beckmannia* Mohanti, 1972.

SYSTEMATICS

Mohanti (1972: 166–7) erected the genus *Beckmannia*, with *Uncinulus minor beckmanni* Schmidt, 1951 as the type species, and assigned some Spanish uncinulids to the same taxon. It now appears it might not have been correct procedure to make a subspecies the type of a new genus (Mohanti 1972: 166); the subspecies should first have been elevated to a species. Although the typical subspecies *Uncinulus minor minor* (Schnur) has not been re-examined by us, as explained below we now believe that *U. m. beckmanni* Schmidt is not even the same genus as *U. m. minor* (now ascribed to *Kransia* Westbroek), and should have been cited as *Beckmannia beckmanni*.

The external characteristics of *Beckmannia* agree closely with the description given by Anderson *et al.* (1969) for their *Markitoechia* species, and our own examination of the Burmese specimen (BB 55550, Anderson *et al.* 1969: pl. 6, figs 1–4) (Fig. 1a–e herein) leads us to the opinion they are congeneric.

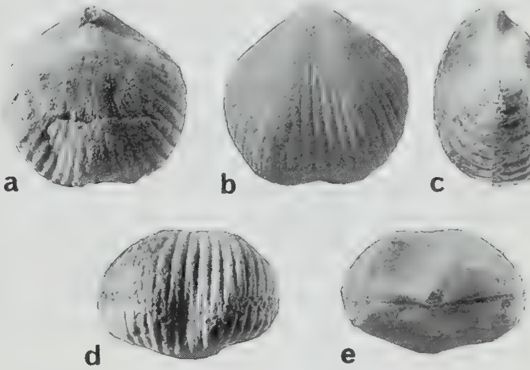

Fig. 1a–e Dorsal, ventral, lateral, anterior and posterior views respectively of specimen BB 55550, from Middle Devonian of Padaukpin, Burma. **Holotype** of *Beckmannia padaukpinensis* sp. nov. Figs 1d, e with dorsal valve at bottom. All × 4.

The three serial sections (Z–1, Z–2, Z–3) of specimen BB 55589C, and its remaining cut surface (marked as N), were examined and are refigured here (Figs 2a–d). The differences between our figures and the figures of serial sections presented by Anderson *et al.* (1969: 139, fig. 4) are clear. In ours the ventral valve has two thin dental plates supporting the teeth, and in the dorsal valve the hinge plate is divided. The median septum is thin and does not support the hinge plate anteriorly. Serial sections of a topotypic specimen of *Beckmannia beckmanni* from Germany (Mohanti 1972: 167, fig. 26 (see Fig. 3 herein); 168, fig. 27), displayed the presence of a cardinal process posteromedially (Fig. 3a). In his original description of *Beckmannia* Mohanti (1972) drew attention to structures associated with the crural bases observed on the 'peels' of serial sections taken from his Spanish specimens (1972: 166, fig. 25). These were referred to as 'an elevated and bilobate cardinal process . . . ' We believe *Beckmannia* has a true apical, striated cardinal process (Fig. 3a), but the structures associated with crural bases should not be termed a

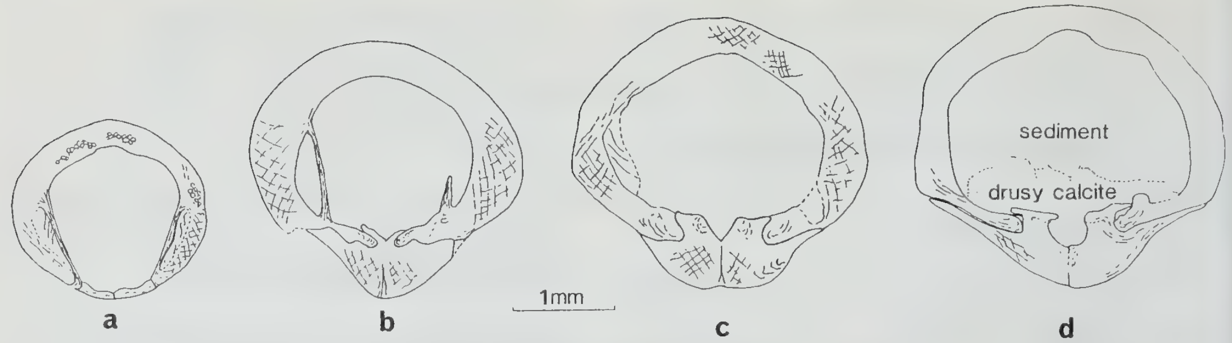

Fig. 2a–d Serial sections × 24 of *Beckmannia padaukpinensis* sp. nov. (called by Anderson *et al.* (1969) 'Markitoechia? cf. *pentagona*'), redrawn using camera lucida from the original 'peels'. (BB 55589C). d = specimen surface N.

cardinal process. Neither the topotype German nor Burmese sectioned specimens display the structures and we now believe it possible that they are no more than representations on the 'peels' of calcite crystals. Thus on examination the internal characters of the Burmese material agree closely with those of the type species of *Beckmannia* and the internal characters of the Spanish specimens assigned to the genus *Beckmannia* (Mohanti, 1972).

During his investigations of uncinulids from the Eifel area of Germany, Westbroek (1967, Enclosure–I) included the typical subspecies '*Uncinulus minor minor*' (Schnur, 1853) (see Schmidt, 1941, 1951) in his new genus *Kransia*, observing that it has a continuous hinge plate; he indicated its range as within the upper Eifelian–Givetian interval. However, as pointed out by Mohanti (1972: 160, 167), this taxon needs further investigation before assigning it to a genus or a stratigraphical range. We believe, however, that the two forms are not even congeneric and should be given full species status, viz. *Beckmannia beckmanni* (Schmidt, 1951) and *Kransia? minor* (Schnur, 1853). *B. beckmanni* is not conspecific with the Burmese specimens so, for the latter, we propose a new species, below.

Beckmannia padaukpinensis sp. nov. Fig. 1a–d

? 1908 *Rhynchonella (Hypothyris) pentagona* (Goldfuss); Reed: 91; pl. 14, figs 15, 15a–b.

1969 *Markitoechia?* cf. *pentagona* (Kayser, 1871); Anderson *et al.*: 139–140; pl. 6, figs 1–4.

HOLOTYPE. BB 55550 from the Padaukpin Limestone, Padaukpin, about 10 miles NE of Maymyo, Central Burma. First satisfactorily illustrated by Anderson *et al.* (1969), above.

DIAGNOSIS. *Beckmannia* with costae and ventral sulcus originating within first 3 mm of growth and having a clearly differentiated sulcate anterior commissure.

COMMENT. The type species, *B. beckmanni*, has costae originating only after about 6 mm of growth and the commissural folding is weak. In other respects the two species are closely comparable.

STRATIGRAPHICAL AND PALAEOBIOGEOGRAPHICAL DISTRIBUTIONS

The type specimens of the type species of *Beckmannia* came from the Upper Givetian 'Flinzkalk' on the east side of the Rhine River near Letmathe, Germany (Schmidt 1951: 89). Mohanti (1972) favoured a Lower Givetian age for *Beckmannia beckmanni* in the context of the general biostratigraphy of the Portilla Limestone Formation of the southern Cantabrian Mountains, Spain, where the Eifelian–Givetian boundary was shown to occur in the Alba syncline.

Ficner & Havlíček (1978: 69) have recorded two species of

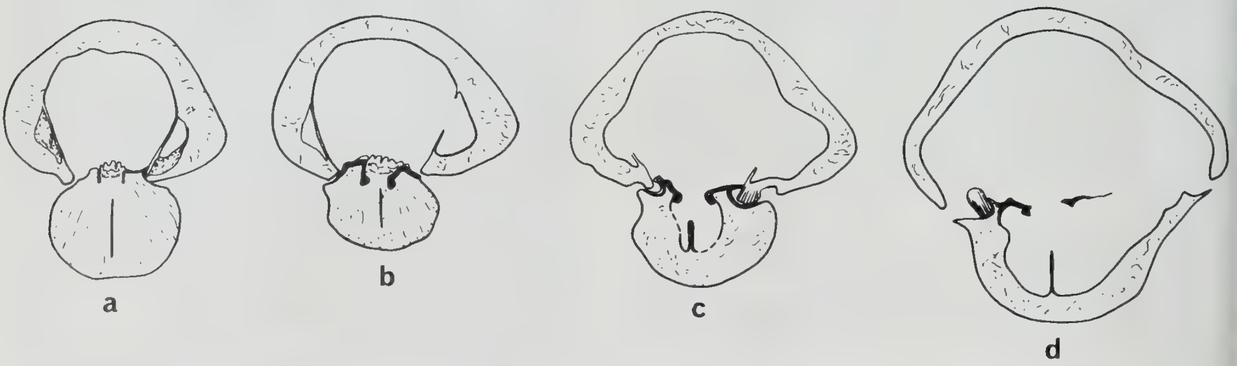

Fig. 3a–d Selected serial sections × 21 of *Beckmannia beckmanni* (Schmidt); topotypic specimen from Germany (Mohanti 1972: fig. 26).

Beckmannia from the late lower Givetian brachiopod assemblages at Čelechovice, Moravia, Czechoslovakia. Sapelnikov *et al.* (1987), while dealing with the Upper Silurian–Middle Devonian brachiopods of the eastern slope of the northern Urals, U.S.S.R., described *Beckmannia angularis* (Phillips 1841) as possibly of Emsian age. If they are right in identifying their Urals specimens as *Terebratula angularis* Phillips, (1841: 89; pl. 35, figs 162a–c), then the British species must also be a record of *Beckmannia*.

This revised occurrence of the uncinulid genus *Beckmannia* in Burma is from an assemblage of brachiopods generally considered as of Eifelian age (Reed 1908, Anderson *et al.* 1969). However, Anderson *et al.* (1969: 117), on admittedly somewhat inadequate evidence derived from the study of specimens of the conodont *Polygnathus*, suggested a correlation of the Burmese occurrences with the Upper Eifelian to Lower Givetian strata of central Europe. Mohanti & Gupta (1987) suggested the possibility of an Eifelian–Givetian boundary within the Padaukpin Middle Devonian strata. A Givetian age for the principal occurrences (Fig. 4) of *Beckmannia* is favoured.

Beckmannia is a rhynchonellid brachiopod having biogeographical affinities with the Rhenish–Bohemian Region of the Old World Realm (Boucot 1975). Struve (1982*a*) favoured the terms Rhenish, Bohemo, Hercynian etc. as restricted to faunal provinces. Information from brachiopods indicates that the Rhenish–Bohemian Region of the Old World Realm extended from parts of the European marine depositional basins eastwards as far as Burma and China (Anderson *et al.* 1969, Zhang Yan 1985, Mohanti & Gupta 1987), while Struve (1982*b*), working on data from well-known European regions, has provided a clear picture of the southeasterly extension of the Middle Devonian 'Rheno-Ardennic' brachiopod biogeography.

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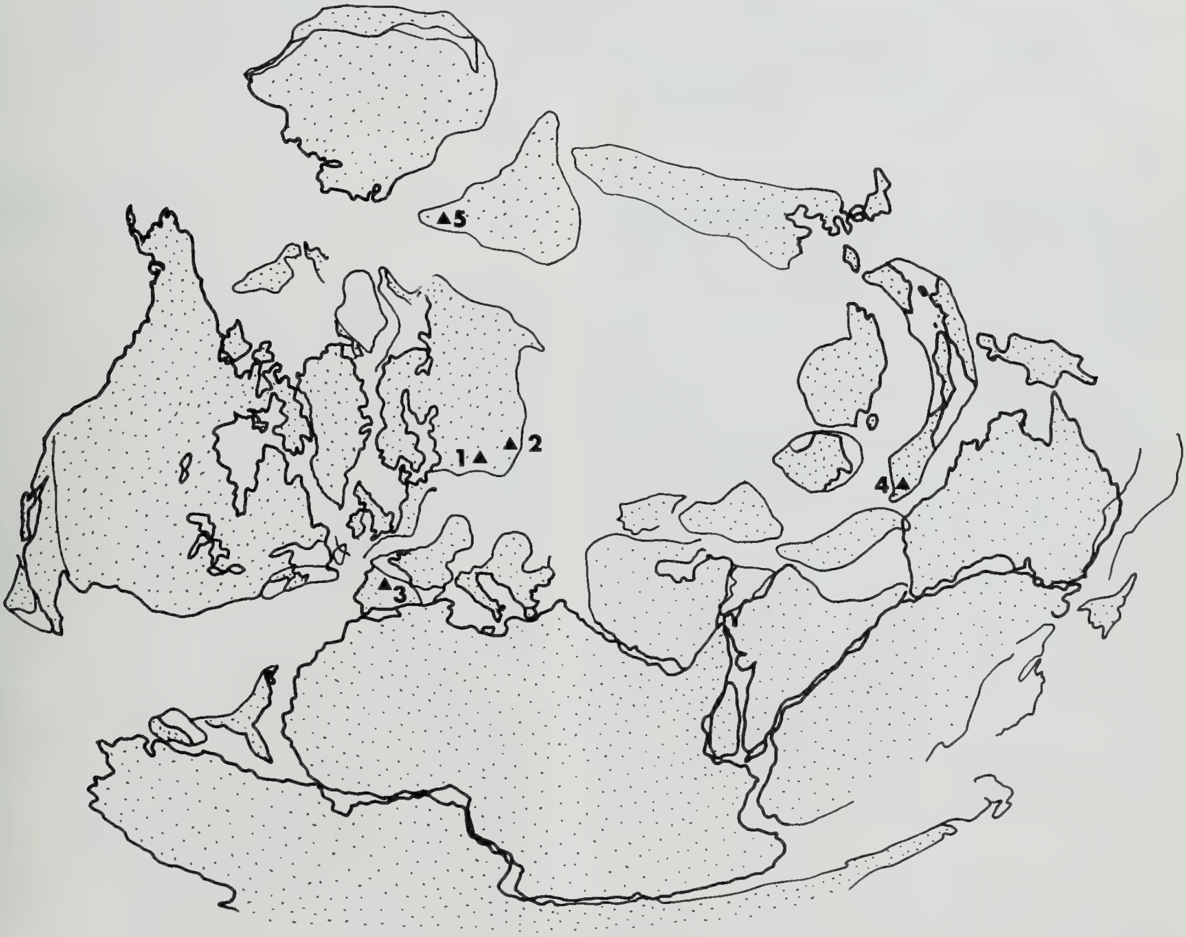

Fig. 4 Givetian palaeogeographical reconstruction (after Scotese & McKerrow, 1990) showing the distribution of known occurances of *Beckmannia*. 1 = type area, Eifel region, Germany; 2 = Celechovice; 3 = Cantabrian Mountains; 4 = Padaukpin, Burma; 5 = northeastern Urals.

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Cheilostome bryozoans from the Upper Cretaceous of the Drumheller area, Alberta, Canada

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Synopsis. As part of a systematic revision of the relatively scarce Cretaceous bryozoan faunas of the North American Western Interior, two encrusting cheilostome species from the lower Maastrichtian part of the Edmonton Group near Drumheller in Alberta are here revised. *Conopeum bicystosum* Allan & Sanderson, 1945 is designated the type species of the new genus *Eokotosokum*, a 'malacostegan' characterized by zooids with well-developed cryptocysts and two large distal spine bases. A second species, *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable, 1981, originally described from the Fox Hills Sandstone of North Dakota, is assigned to *Villicharixa* Gordon, 1989, on account of the numerous small spine bases which are obscured by a ferruginous crust in the holotype specimen. Both *Eokotosokum bicystosum* and *Villicharixa lintonensis* lack ovicells and are inferred to have possessed planktotrophic cyphonautes larvae, in contrast to the majority of contemporaneous European species which had ovicells and non-planktotrophic larvae. They probably inhabited a brackish estuarine environment. Reasons for the depauperate bryozoan fauna of the Western Interior Cretaceous Seaway are discussed in brief.

INTRODUCTION

In spite of extensive searching and collecting, few bryozoans have been encountered in the Cretaceous of the Western Interior of North America. Their scarcity is sufficiently striking, especially in comparison with western Europe (e.g. Voigt, 1979, 1981, 1983), to require explanation. Although a few possibilities are suggested below, the systematics of the bryozoans present in the Western Interior must be re-evaluated on a consistent comparative basis before palaeobiologically reasonable possibilities can be fully explored. The purpose of this paper is to describe one of the most abundant bryozoan occurrences in the region.

Conopeum bicystosum Allan & Sanderson, 1945, was originally described from the Edmonton Group of central Alberta on the basis of very limited material. More extensive collections from Alberta confirm that this species greatly dominates the Maastrichtian bryozoan fauna of the Edmonton Group but requires re-assignment to a new genus, *Eokotosokum* (p. 17). One specimen, however, belongs to a different species, *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable, 1981, originally described from an approximately correlative horizon in North Dakota, and here re-assigned to *Villicharixa* Gordon, 1989.

The results of the present study fall into the same pattern as was suggested by a preliminary survey of the Western Interior Cretaceous bryozoan literature (R.J. Cuffey, unpublished), namely a small number of distinctive species, which are difficult to assign generically, occur. This may imply the occasional establishment of local endemic populations, scattered geographically and geochronologically up and down the Western Interior Cretaceous seaway. The region's bryozoan fauna thus contrasts markedly with the more diverse and abundant bryozoans evolving contemporaneously in Europe. Explanations for this contrast have tended to focus upon the inferred harsh or stressful conditions which may have prevailed within the seaway, such as lack of suitable substrates on its extensive soft 'soupy' bottoms, and extreme fluctuations in salinity or dissolved oxygen concentration beyond the tolerance limits within which most bryozoans could survive (Fig. 1) (Frey, 1972; Hattin, 1975, 1982; Kauffman, 1975, 1986; Bottjer *et al.*, 1978; Arthur & Schlanger, 1979; Arthur *et al.*, 1981; Kauffman & Fürsich, 1982; Bottjer, 1986; Diner, 1986; Gautier, 1986; Sageman, 1986; Watkins, 1986; Wright, 1987; Dean *et al.*, 1988). The regional palaeogeography established a precipitation gradient across the seaway. Runoff from the west diluted its surface waters, thereby possibly killing bryozoan larvae entering the seaway from other regions. Evaporation in the east increased salinity, hence density, and this created a sluggish bottom flow back downslope, and eventually an upwelling enhancing productivity. Phytoplankton and terrigenous sediment both made for murky waters; decay of terrestrial plant and phytoplanktonic debris depleted oxygen in the seaway's bottom waters. This combination of elevated salinity, high turbidity, very soft muddy bottoms, and poor circulation would have been lethal for most bryozoan colonies, except those on the refuges provided by giant shells or free-swimming ammonites.

Recently, an additional explanation is suggested by modelling Cretaceous oceanic circulation (Barron & Peterson, 1989, 1990), which suggests that prevailing surface currents flowed away from North America and towards Europe, a pattern which would prevent bryozoan larvae from being transferred westward out of the high diversity European region. An interesting comparison might be made with

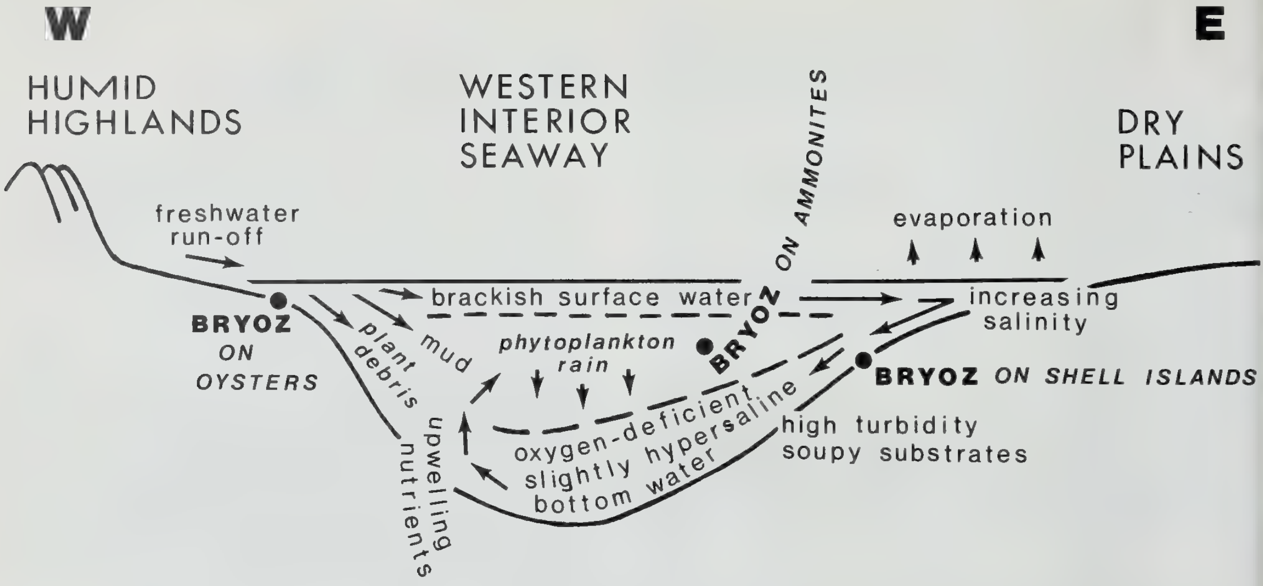


Fig. 1 Schematic cross section of the Western Interior Cretaceous Seaway showing regional palaeoenvironmental factors interacting to produce local habitat effects severely limiting bryozoan development, except where indicated by 'BRYOZ'. Western shoreline bryozoan occurrence exemplified by this paper and Cuffey *et al.* (1981); central occurrence by Cuffey (1990) and Gill & Cobban (1966); eastern occurrence by Kauffman (1986).

present-day reef corals in the Indo-Pacific; Jokiel (1989) has suggested that movement of rafted corals and drifted larvae occurs predominantly away from peripheral areas of low coral diversity (cf. Western Interior seaway) and towards centres of high diversity (cf. Europe) which act as areas of species accumulation. However, there is as yet no good evidence from temporal and geographical distributions to suggest that regions like the Western Interior seaway were source areas for the large numbers of bryozoan species present in Cretaceous rocks of Europe.

Another observation which may have some bearing on the low diversity of bryozoan species in the Western Interior is that most (or all) of the cheilostome species described lack ovicells and can therefore be inferred to have possessed long-lived, planktotrophic, cyphonautes larvae (see Taylor, 1987, 1988). This contrasts with the European Upper Cretaceous where the great bulk of species have ovicells and consequently possessed short-lived, non-planktotrophic, coronate larvae. Rates of speciation are predicted to have been higher in non-planktotrophic groups than in planktotrophic groups (Taylor, 1988), and it may also be significant that planktotrophic groups at the present day are subordinate to non-planktotrophic groups in most environments except nearshore and estuarine environments—as noted below (p. 16), the Drumheller bryozoans come from a brackish environment.

GEOLOGICAL SETTING

Location and localities

The bryozoans studied herein come from near Drumheller in central Alberta, western Canada, where the Red Deer River has incised a valley 120 m (400 ft) below the surrounding plains (Figs 2 & 3). Specific localities are as follows:

1. *Horseshoe Canyon (HS).* Badlands and elongate ravine draining northward into Kneehills Creek (tributary to the Red Deer River), 13·3 km (8·3 miles) west-southwest of the bridge carrying Alberta Highway 9 over the Red Deer River in the centre of Drumheller. Bryozoans (types of *Eokotosokum bicystosum*) on rare oyster shells obtained 3·5 km (2·2 miles) N25°W of parking viewpoint where Alberta Highway 9 runs along the badlands rim (Fig. 3A). Bryozoan locality at Universal Transverse Mercator coordinates 5700900 m N, 368000 m E, in the western branch of this canyon, as marked on the 1990 Drumheller 1:50,000 topographic map (Energy Mines & Resources Canada); land survey coordinates SW corner SE1/4 sec. 33, Tp. 29 [not 28], R.21W4.
2. *Horsethief Canyon (HT).* Badlands forming eastern side of Red Deer River valley, 13·7 km (8·5 miles) northwest of the provincial Highway 9 bridge across the Red Deer River in the centre of Drumheller. Bryozoans on abundant oyster fragments in thin lens at 756 m (2480 ft) elevation, on north side of badlands hill (Fig. 3B) located 200 m (650 ft) S45°W of parking viewpoint where gravel road ends at rim of valley. Bryozoan locality at Universal Transverse Mercator coordinates 5711600 m N, 370500 m E, as marked on the 1989 Munson 1:50,000 topographic map (Energy Mines & Resources Canada); land survey coordinates centre E1/2 NE1/4 sec. 34, Tp. 30, R.21W4.
3. *Drumheller area (DR).* Badlands and tributaries along the Red Deer River valley near Drumheller. Bryozoans on oyster shells found by various amateur and commercial collectors in the area; precise locality details unavailable.

Stratigraphy and palaeoecology

The Drumheller bryozoans are found in the lower oyster bed of the Drumheller marine tongue coming into the Horseshoe

Canyon Formation of the Edmonton Group (Jackson *et al.*, 1981; Harvey *et al.*, 1982; Irish, 1970; Stelck *et al.*, 1972; Allan & Sanderson, 1945). The tongue is of early Maastrichtian age, and thus is near (but not exactly at) the top of the Upper Cretaceous series here (Fig. 4). The regional stratigraphy is characterized by diachronous intertonguing of the major lithofacies. These were deposited along a deltaic shoreline retreating southeastwards, but frequently fluctuating locally in response to variations in sediment supply, coastal-ground compaction or subsidence, regional tectonism, and possibly also eustatic sea-level changes.

The great bulk of the Edmonton Group is made up of the Horseshoe Canyon Formation, 275 m (900 ft) thick around Drumheller, and consisting of complexly interlensing and interbedded grey, tan and brown shales, mudstones, and soft sandstones, with scattered thin lenses of concretionary ironstone and several beds of subbituminous coal. It is overlain by the thin Whitemud Sandstone, Battle Shale, and dinosaur-bearing Scollard Beds. It is underlain by the fully marine, but shallow water, dark-grey Bearpaw Shale, 150 m (500 ft) thick in this vicinity; their contact is an intertonguing transitional zone, and the Drumheller marine tongue is simply a somewhat later and more extensive part of this formational interface on a regional scale (Fig. 4). The Horseshoe Canyon Formation has yielded various continental fossils: dinosaurs, small vertebrates, freshwater molluscs, woody plants, and palynomorphs (Allan & Sanderson, 1945; Irish, 1970; Srivastava, 1970; Harvey *et al.*, 1982; Gross, 1985). These indicate a humid subtropical climate at the time when *Eokotosokum bicystosum* inhabited the adjacent bays. Especially in its lower portion transitional into the Bearpaw Shale, the Horseshoe Canyon Formation represents deposition in a continental to paralic delta complex, with many different subenvironments recognizable (Irish, 1970; Shepheard & Hills, 1970; Harvey *et al.*, 1982; Rahmani & Hills, 1982; Waheed & Miall, 1985).

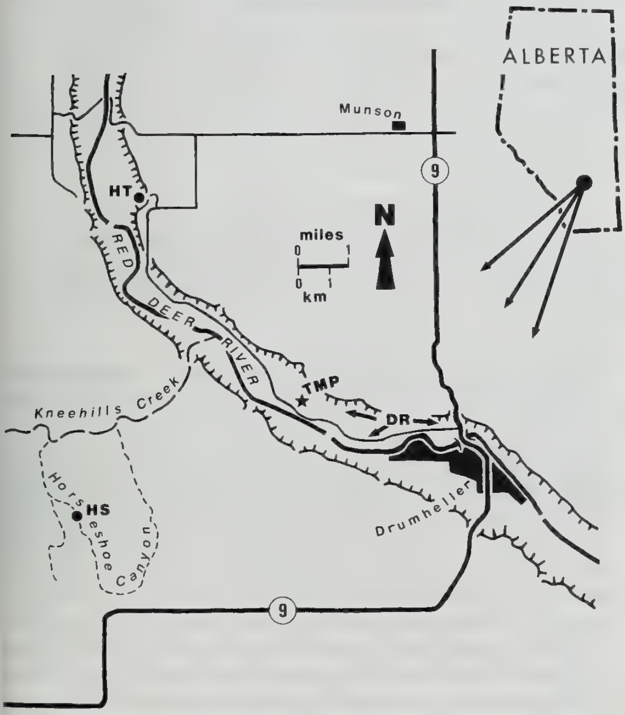


Fig. 2 Sketch map of the Drumheller region, central Alberta, Canada, showing bryozoan localities HS, HT and DR (see text), Tyrrell Museum of Palaeontology (TMP), and rim of valley badlands at edge of the flat plains above the Red Deer River.

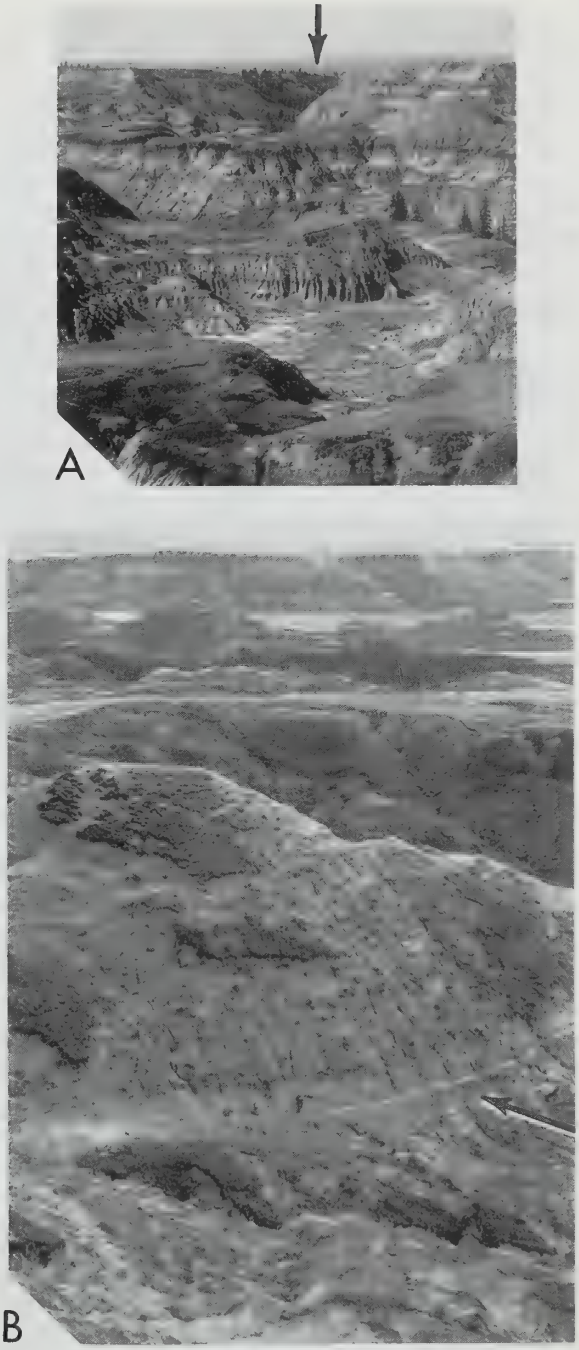


Fig. 3 Views of Drumheller bryozoan localities. A, locality HS. B, locality HT. Arrows indicate positions of collecting sites within the intricately sculptured badlands, as seen from the parking viewpoints where the footpaths to the sites begin.

The badlands and valley wall at locality HT are made up entirely of the Horseshoe Canyon Formation (Jackson *et al.*, 1981; Stelck *et al.*, 1972). Most of the exposures at locality HS

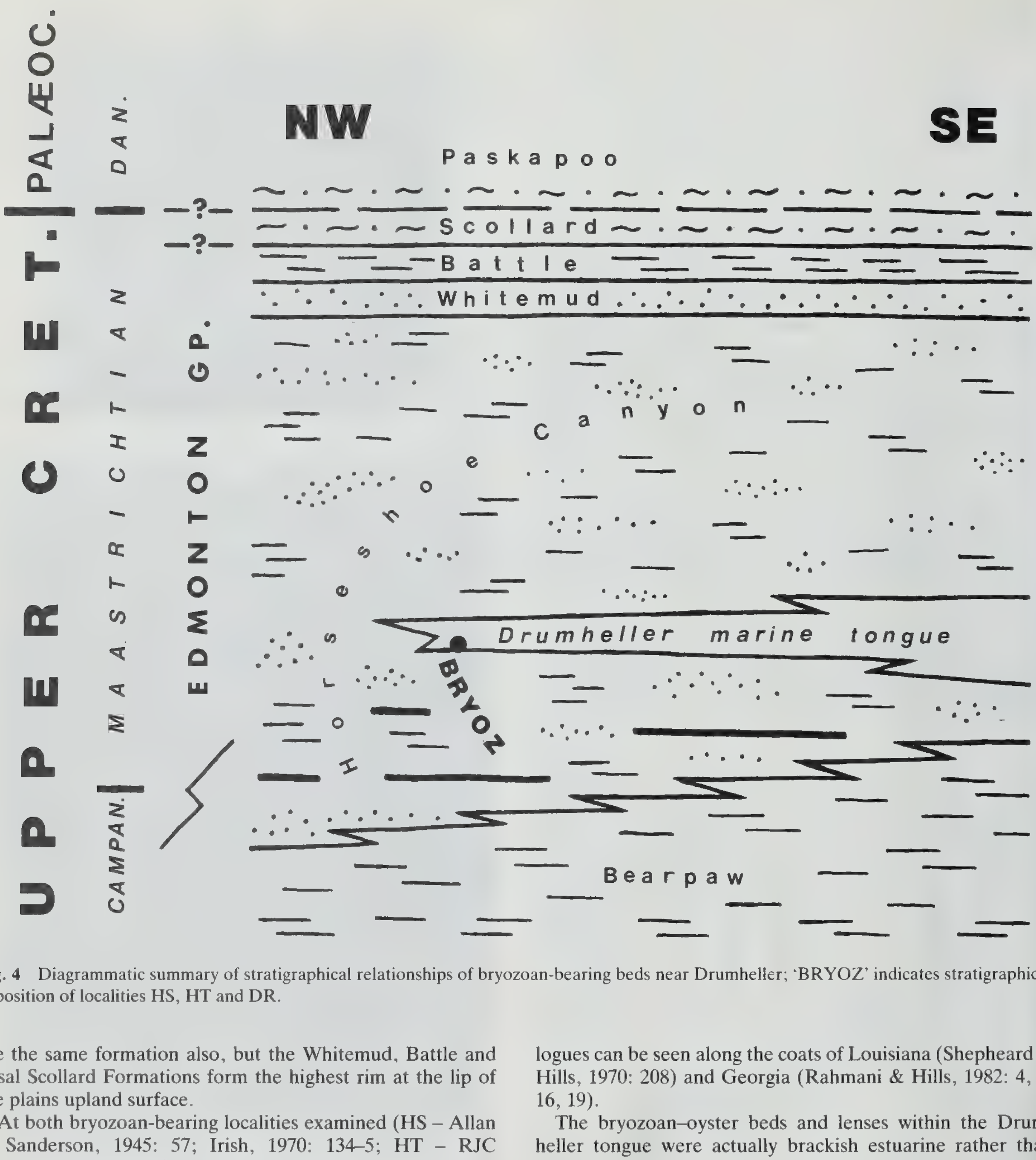


Fig. 4 Diagrammatic summary of stratigraphical relationships of bryozoan-bearing beds near Drumheller; 'BRYOZ' indicates stratigraphical position of localities HS, HT and DR.

are the same formation also, but the Whitemud, Battle and basal Scollard Formations form the highest rim at the lip of the plains upland surface.

At both bryozoan-bearing localities examined (HS – Allan & Sanderson, 1945: 57; Irish, 1970: 134–5; HT – RJC personal observations), the Drumheller marine tongue consists of a thin (0·3–1·0 m = 1–3 ft) lower oyster shell-bed entirely of *Crassostrea glabra coalvillensis* (some encrusted by *Eokotosokum bicystosum*) in a silt matrix, a middle unfossiliferous mudstone (5–6 m = 15–18 ft), and an upper sandstone (0·3–1·0 m = 1–3 ft) with fragmentary *Corbicula occidentalis ventricosa* (but no encrusting bryozoans). Elsewhere, the tongue is structured differently and contains other brackish or marine molluscs, ray-teeth, fish-scales, and even foraminiferans (Allan & Sanderson, 1945; Irish, 1970: 136–7; Stelck *et al.*, 1972: 18–19, 46–8). These deposits represent short-lived, temporary, brackish bays or estuaries indenting the overall deltaic coastline. Modern environmental analogues can be seen along the coats of Louisiana (Shepheard & Hills, 1970: 208) and Georgia (Rahmani & Hills, 1982: 4, 9, 16, 19).

The bryozoan–oyster beds and lenses within the Drumheller tongue were actually brackish estuarine rather than euhaline marine, as indicated by the extremely low diversity of their fauna. All but one of the many Drumheller bryozoan colonies represent the single species *Eokotosokum bicystosum*, and virtually all of the shells occurring with them are the one oyster *Crassostrea glabra coalvillensis*. None of the shells collected in place were bored, unlike some of the North Dakota bryozoan-encrusted oysters with possible ctenostome (*Orbignyopora*) or phoronid (*Talpina*) borings (Cuffey *et al.*, 1981). Such a low-diversity oyster–bryozoan assemblage closely resembles that of Pleistocene and Recent Atlantic coastal estuaries where the abundant oyster *Crassostrea virginica* bears crusts of only three or so membraniporoid species (Mapleton & Cuffey, 1992; Butler & Cuffey, 1991;

Kent, 1988; Osburn, 1944; Winston, 1977).

Finally, note must be taken of a surprising peculiarity endemic to Drumheller stratigraphic literature: namely, calling the oyster shell fragments 'ostracods' (even as recently as Harvey *et al.*, 1982: 3–4, 18).

Preservation and methods

Preservation of bryozoans encountered in the Western Interior Cretaceous varies enormously from site to site. Some localities yield obscure remnants identifiable only to family, like the bryozoans found on baculitid ammonites in Colorado and Wyoming (Cuffey, 1990; Gill & Cobban, 1966). Others furnish moderately well-preserved calcareous skeletal fossils, such as those encrusting oysters in North Dakota and Kansas (Cuffey *et al.*, 1981; Scott, 1970). The Drumheller bryozoans exemplify the latter style of preservation, and so can be studied using techniques like scanning electron microscopy now standard in bryozoology (Taylor, 1990). The capability of scanning uncoated specimens using back-scattered electron imaging (Taylor, 1986*a*) has made detailed study and accurate illustration of the type specimens of *Eokotosokum bicystosum* possible.

SYSTEMATIC PALAEONTOLOGY

Specimen repositories and abbreviations. Materials examined for this paper are housed in the following collections: BMNH, The Natural History Museum, London; PBRC-PSU, Paleobryozoological Research Collection at Pennsylvania State University, University Park, State College, Pennsylvania; ROM, Royal Ontario Museum, Toronto; SMC, Sedgwick Museum, Cambridge; TMP, Tyrrell Museum of Palaeontology, Drumheller; USNM, National Museum of Natural History, Smithsonian Institution, Washington.

Order **CHEILOSTOMIDA** Busk, 1852
Suborder **MALACOSTEGINA** Levinsen, 1902
Superfamily **MEMBRANIPOROIDEA** Busk, 1854
Family **ELECTRIDAE** Stach, 1937

Genus ***EOKOTOSOKUM*** nov.

TYPE SPECIES. *Conopeum bicystosum* Allan & Sanderson, 1945; Lower Maastrichtian, central Alberta, Canada.

NAME. *Eokotosokum* is a classicized version of the Blackfoot Indian word-combination meaning ancient stone sheets, alluding to the encrusting sheet-like form of the colonies. The Blackfeet were the overall tribe ranging through the type region in aboriginal times.

DIAGNOSIS. Electrid genus with autozooids having a shelf-like, pustulose cryptocyst, an imperforate gymnocyst and a pair of large distolateral spine bases; pore chambers apparently absent; ancestrula budding a distal and a proximal periancestrular zooid; colonies sheet-like, initially uniserial but predominantly multiserial, unilamellar or thinly multilamellar.

REMARKS. This new genus is proposed because *Conopeum bicystosum* is sufficiently distinctive from, and cannot be easily assigned to, any existing genus of cheilostomes.

The lack of ovicells in any of the large suite of specimens available implies that *Eokotosokum bicystosum* possessed non-brooded, planktotrophic larvae. Therefore, the species belongs to a primitive, paraphyletic grouping of anascan cheilostomes termed 'malacostegans' (Taylor, 1987). The occurrence of a proximal periancestrular bud, a feature lost in the great majority of advanced brooding cheilostomes, further supports this interpretation, and lack of a twinned ancestrula allows assignment to the more primitive of the two currently recognized malacostegan families, the Electridae.

Comparison with the type species of existing nominal genera of 'malacostegan' cheilostomes reveals significant differences between these and *Eokotosokum*. The pertinent genera with similar colony and zooid morphologies are *Conopeum, Charixa, Spinicharixa, Wawalia, Electra* and *Biflustra* (see Taylor, 1987) and *Villicharixa* Gordon, 1989. *Eokotosokum* shares with the type species of *Conopeum*, the Recent *C. reticulum* (Linnaeus), a reduced gymnocyst, a broad pustulose cryptocyst, and the absence of pore chambers. However, the two genera differ in the presence of prominent spine bases in *Eokotosokum*, closure plates in *Conopeum*, and in details of their early budding pattern: the ancestrula of *Conopeum* buds a proximal and two distolateral zooids whereas that of *Eokotosokum* buds a proximal and one distal zooid. The type species of *Charixa, C. vennensis* Lang from the Albian, is poorly known (Taylor, 1986*b*), but it and other species assigned to *Charixa* have better-developed gymnocysts and less well-developed cryptocysts than *Eokotosokum*. Although distolateral spine bases occur sporadically in zooids of *Charixa lindiensis* Taylor, resembling those of *Eokotosokum*, species of *Charixa* possess pore chambers which are absent in *Eokotosokum*. *Spinicharixa*, type species *S. pitti* Taylor from the Lower Cretaceous, has multiple spine bases surrounding the opesia (see p. 22), and closure plates, and the ancestrula buds only a distal zooid. Early budding pattern in *Wawalia*, type species *W. crenulata* Dzik from the Lower Cretaceous, also differs from that observed in *Eokotosokum*, and *Wawalia* is further distinguished by striations on the cryptocyst and its fissured gymnocyst. *Electra*, type species the Recent *E. verticillata* (Ellis & Solander)(=*E. pilosa* (Linnaeus)), shares with *Eokotosokum* a 'compound multiserial' growth-form (Silén, 1987), but again differs in early budding pattern and also lacks a cryptocyst and distolateral spine bases, and has a porous gymnocyst. Finally, *Biflustra*, type species the Recent *B. savartii* (Audouin), differs from *Eokotosokum* in having no gymnocyst and, importantly, in possessing a twinned ancestrula. *Villicharixa*, type species *Membraniporina strigosa* Uttley from the Pleistocene and Recent of New Zealand, has multiple spine bases and a poorly-developed cryptocyst (see p. 22).

These comparisons provide justification for the proposal of the new genus *Eokotosokum*. Although initially monospecific, restudy of the diverse but poorly-known membraniporimorph cheilostomes of Cretaceous to Recent age can be expected to reveal additional congeneric species.

Eokotosokum bicystosum (Allan & Sanderson, 1945)
Figs 5–12

1931 *Conopeum bicystosum* Sanderson: 1254 [nomen nudum].
1945 *Conopeum bicystosum* Allan & Sanderson: 89; pl. 7.

HOLOTYPE. ROM 5337.ct.(a); Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian); locality HS, near Drumheller, Alberta; J.O.G. Sanderson Collection. Although Allan & Sanderson (1945) mentioned only a holotype specimen under this registration number, the ROM collections contain two specimens, encrusting separate oyster shells, labelled as cotypes (i.e. syntypes). One of these specimens (Fig. 7) corresponds closely with their illustration (1945: pl. 7) which is, however, reproduced upside down; this specimen is taken to be the intended holotype.

Paratype. The second specimen in the ROM Collection – 5337.ct.(b) – includes a less well-preserved colony of *E. bicystosum*, interpreted as a paratype, together with the colony of *Villicharixa lintonensis* described below.

Other material. BMNH D57396–401, D59482–3, locality DR; TMP 91.136.1 and 91.136.2, locality DR; TMP 91.136.3, locality HT; PBRC-PSU ALBDRU-DR and ALBDRU-HT suites, localities DR and HT respectively. All from the Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian), near Drumheller, Alberta, Canada.

Description. Colonies are encrusting, sheet-like (Figs 5A, 8A), initially uniserial (Figs 9A, 10) but predominantly multiserial, unilamellar or thinly multilamellar (Fig. 6). All available specimens are incomplete colonies characteristically preserved as irregular patches of 10 or more zooids encrusting oyster shells, abraded at patch edges, and representing portions of larger, fragmented colonies. Recognizable growing edges have not been observed. The rarely visible early zooids are arranged in two uniserial branches originating from the distal and proximal ends of the ancestrula (Figs 9, 10). Distolateral budding from post-ancestrular zooids causes multiplication of branch number to give a multiserial colony of the compound type (*sensu* Silén, 1987); intact colonies may have been roughly circular in outline and centred on the ancestrula. In multiserial unilamellar colonies, zooids are arranged in several series paralleling colony growth direction. Zooids of adjacent rows tend to alternate, thus yielding an approximately quincuncial pattern. Multilamellar colonies (Fig. 6) are common and apparently develop by intracolonial overgrowth but do not attain massive thicknesses. Zooids in overgrowths are typically more irregular in shape (some even having re-entrant angles), more disorderly in arrangement and more loosely-packed than are zooids in the basal layers of colonies.

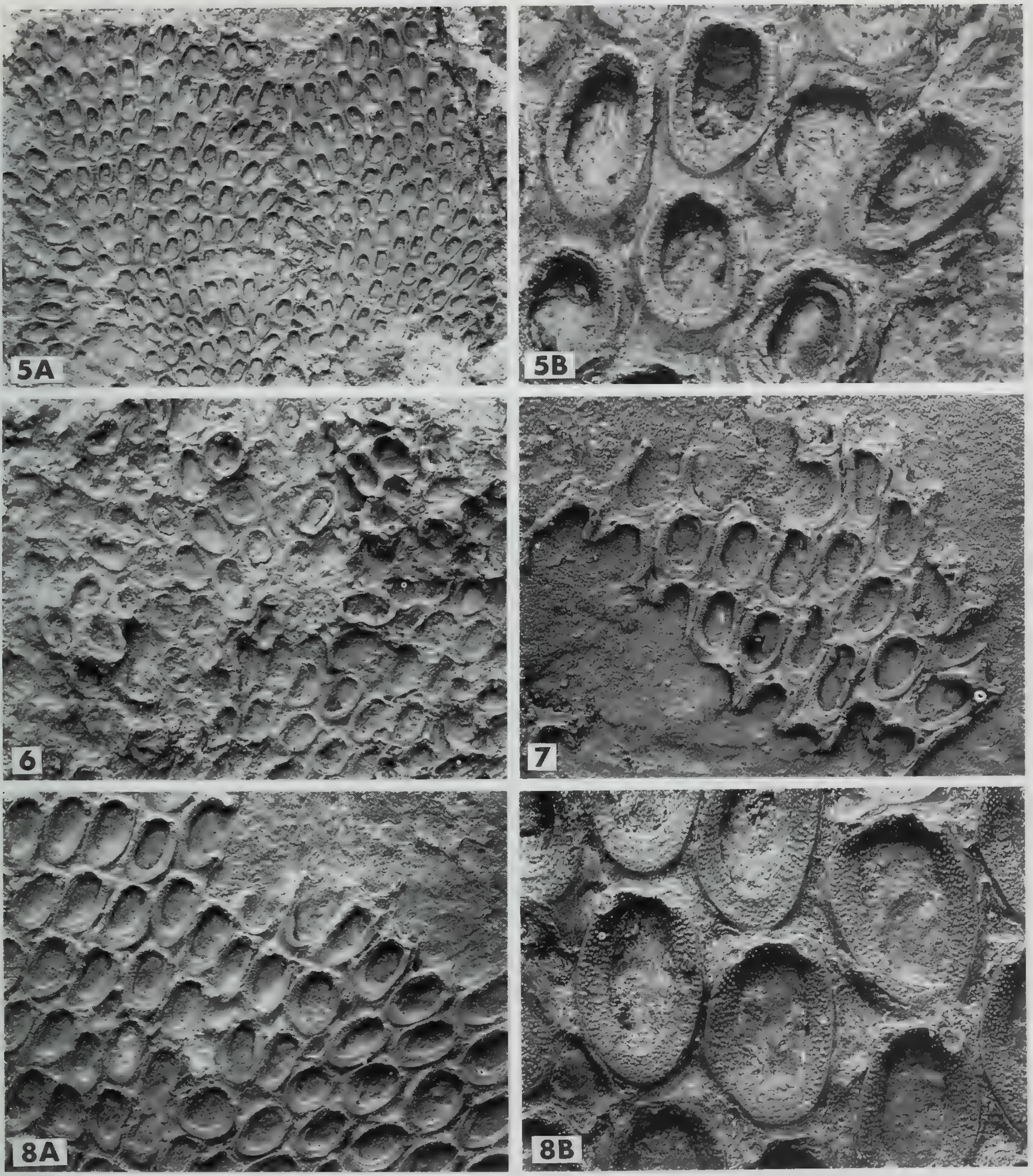
Autozooids have a longitudinally elongate, ovoidal to rectangular outline shape, about 1·5 times as long as wide, and are moderately small (Table 1). Most of the frontal area of the zooid is occupied by the opesia which is also longitudinally ovoidal in shape but is slightly square-ended in most zooids (Figs 5B, 8B). The cryptocyst forms a well-defined shelf around the opesia and is generally at its broadest proximally and narrowest distally. Proximal and lateral parts of the cryptocyst slope gently inwards, whereas the distal part is more steeply sloping. Prominent, evenly-sized pustules are arranged in 6 or more alternating rows on the cryptocyst (Fig. 8B). The gymnocyst forms a small area of smooth calcification outside the cryptocyst. It is usually most extensive proximally and is reduced laterally and distally to a narrow zone dipping steeply into the furrows that separate the zooids. A distolateral pair of spine bases occurs on the cryptocyst–gymnocyst boundary, indenting the cryptocyst and apparently causing the square-ended shape of the opesia (Fig. 11). They are crater-like in form, large (about 0·03 mm maximum diameter), and elongated parallel to the cryptocyst–gymnocyst boundary and hence sub-transversely or obliquely to the long axis of the zooid. The basal walls of at least some zooids are completely calcified. Pore chambers have not been observed in spite of the presence of numerous abraded zooids in which they should be visible if developed. Closure plates are absent. Ovicells do not occur. Intramural buds ('regenerations') are moderately uncommon and are recognizable by the occurrence of a secondary ring-like cryptocyst inside that of the host zooid (Fig. 5B). Some intramural buds have a greater height than the host zooid. These eruptive buds are possible origins of intracolony overgrowths. Whereas eruptive intramural buds possess spine bases and appear to be autozooids, the few observed non-eruptive intramural buds lack spine bases and may be kenozooids. The polarity of eruptive intramural buds, determined by the position of the spine bases, can be oblique to that of the host zooid.

The ancestrula is small (Table 1), longitudinally ovoidal in outline, and has a subcircular opesia which occupies over half of the frontal area (Fig. 9B). Like the post-ancestrular zooids, it has a pustulose, shelf-like cryptocyst, an inextensive gymnocyst best developed proximally, and a pair of distolateral spine bases. However, an additional pair of spine bases appears to occur proximolaterally in one partly sediment-obscured ancestrula and in its daughter zooids. The ancestrula gives rise to two periancestrular daughter zooids, one distally and one proximally. These early zooids initiate a primary zone of astogenetic change, encompassing at least six generations, through which zooid size increases progressively.

Kenozooids and putative kenozooids of varying types can be distinguished by their lack of spine bases, and generally smaller size, irregularity and reduced calcification compared to autozooids. Some are 'vicarious' (Fig. 12B), intercalated in the normal budding sequence of the autozooids, but in areas where spatial restrictions seem to have prohibited autozooid formation; others are distinctly 'adventitious' (Fig. 12A) and occupy interopesial areas on the colony surface, while some appear to be intermediate in that they have small bases in contact with the substratum but expand frontally across interopesial areas. A single large vicarious kenozooid (Fig. 12B) has been observed in which the cryptocyst is substantially broadened distally. Some of the adventitious

Table 1 Zooidal dimensions (mm) in *Eokotosokum bicystosum* (Allan & Sanderson). All measurements of post-ancestrular zooids are from the holotype colony. Abbreviations: $\bar{x}$ = mean; r = observed range; SD = standard deviation; CV = coefficient of variation; N = number of zooids measured.

	$\bar{x}$	r	SD	CV	N
zooidal length	0·407	0·33–0·53	0·046	11·4	15
zooidal width	0·277	0·23–0·38	0·034	12·3	15
opesial length	0·290	0·26–0·32	0·017	5·8	15
opesial width	0·174	0·12–0·21	0·021	12·1	15
ancestrular length	0·16	0·16	–	–	3
ancestrular width	0·13	0·12–0·14	–	–	3
ancestrular opesial length	0·09	0·09	–	–	2
ancestrular opesial width	0·09	0·09	–	–	2

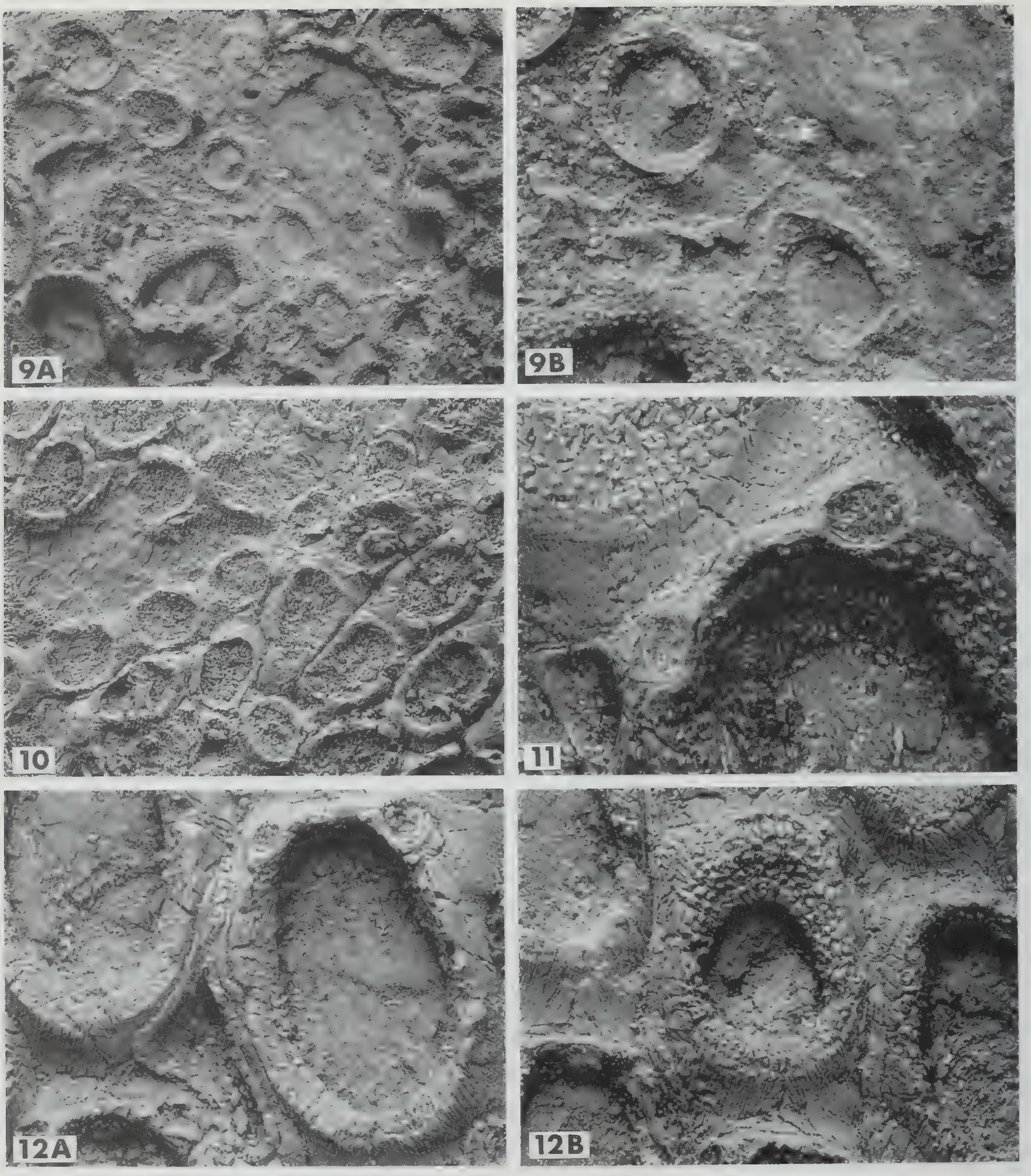


Figs 5–8 *Eokotosokum bicystosum* (Allan & Sanderson), L. Maastrichtian, Edmonton Group, Horseshoe Canyon Formation, Drumheller marine tongue; Drumheller area, Alberta. Scanning electron micrographs of uncoated specimens imaged using back-scattered electrons. Fig. 5, TMP 91.136.1 (see also Fig. 12); 5A, part of a large colony, × 12; 5B, autozooids, one (centre bottom) with a 'regeneration', × 85. Fig. 6, TMP 91.136.2 (see also Fig. 9), colony with overgrowths, × 25. Fig. 7, ROM 5337.ct.(a), part of the holotype colony, × 35. Fig. 8, BMNH D57396 (see also Fig. 11); 5A, autozooids and kenozooids near broken edge of colony, × 27; 5B, autozooids showing pustulose cryptocysts, × 80.

and intermediate kenozooids lack both gymnocysts and pustulose cryptocysts, and possess only basal walls and reduced vertical walls; abrasion may have accentuated the vestigial morphology of these kenozooids. A second possible source of multilamellar colony growth could be budding from adventitious and intermediate type kenozooids.

Avicularia are absent.

Remarks. The original description of *E. bicystosum* by Allan & Sanderson (1945) is reasonably accurate but fails to



Figs 9–12 *Eokotosokum bicystosum* (Allan & Sanderson), L. Maastrichtian, Edmonton Group, Horseshoe Canyon Formation, Drumheller marine tongue; Drumheller area, Alberta. Scanning electron micrographs of uncoated specimens imaged using back-scattered electrons. Fig. 9, TMP 91.136.2 (see also Fig. 6); 9A, early zooids arranged in a uniserial line running top left to bottom right of the micrograph, × 70; 9B, ancestrula (top left) with proximal bud (bottom right), × 170. Fig. 10, TMP 91.136.3, early zooids of another colony, × 56. Fig. 11, BMNH D57396 (see also Fig. 8), large distolateral spine bases of an autozooid, × 310. Fig. 12, TMP 91.136.1 (see also Fig. 5), kenozooids; 12A, small kenozooid with reduced calcification infilling area between autozooids, × 180; 12B, large, vicarious kenozooid, × 173.

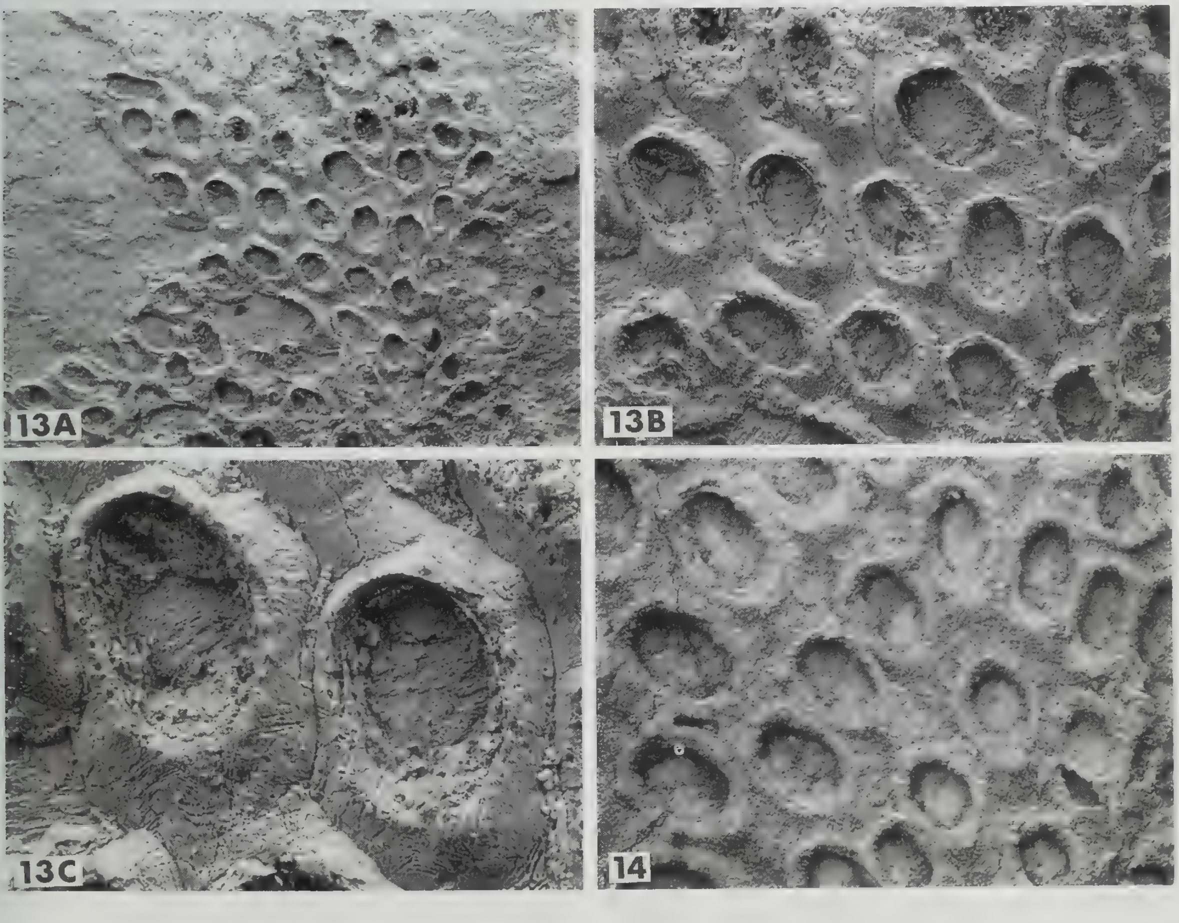
identify the occurrence of the large distolateral spine bases which are very characteristic of the species and presumably signify the presence during life of substantial upright or perhaps overarching spines in the orificial region. Although it is possible that Allan & Sanderson described the spine bases as interopesial spaces, this description could equally apply to the adventitious kenozooids. Many of the morphological features of this and similar cheilostomes cannot be adequately resolved using an optical microscope and full description demands the use of scanning electron microscopy.

Only one other formally described cheilostome species is known to occur in the uppermost Cretaceous of the Western Interior province. This is *Villicharixa lintonensis* (Cuffey, Feldmann & Pohlable, 1981), distinguished from *E. bicystosum* by the presence of a gymnocystal tubercle on the proximal edge of the opesia, multiple small spine bases encircling the opesia, a negligible cryptocyst, and a different early budding pattern (see p. 22). Elsewhere, Upper Cretaceous membraniporimorph bryozoans have been described from the Ripley Formation of Tennessee (Canu & Bassler, 1926), and from many localities in Europe (e.g., see Voigt, 1979, 1981, 1983). Few of these species possess distolateral spine bases of the type characterizing *E. bicystosum. Membranipora gegania* Brydone, from the lower Maastrichtian of Norfolk, England, does have a distolateral pair of spine bases, but study of the holotype (SMC B36555) has revealed several differences from *E. bicystosum*: the autozooids in *M. gegania* are larger and broader, small ovicells are present, and large pore chambers occur. *Membranipora frontalis* Levinsen, described from the lower Maastrichtian of Denmark, seems also to have broader autozooids than *E. bicystosum* and apparently possesses pore chambers; it may be a senior synonym of *M. gegania*..

DISTRIBUTION. Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian); localities HS, HT and DR, near Drumheller, Alberta, Canada. Also recorded by Sanderson (1931: 1254) and Allan & Sanderson (1945: 79) from the Fox Hills Sandstone (lower to middle Maastrichtian) of southern Alberta; however, this record requires confirmation as the specimens have not been figured and may alternatively be *Villicharixa lintonensis*.

Genus ***VILLICHARIXA*** Gordon, 1989

TYPE SPECIES. *Membraniporina strigosa* Uttley, 1951, by original designation (Gordon, 1989); Pleistocene and Recent of New Zealand.



Figs 13–14 *Villicharixa lintonensis* (Cuffey, Feldmann & Pohlable). Fig. 13, ROM 5337.ct.(b), L. Maastrichtian, Edmonton Group, Horseshoe Canyon Formation, Drumheller marine tongue; Drumheller area, Alberta. Scanning electron micrographs of uncoated specimen imaged using back-scattered electrons; 13A, general view of colony encrusting the same substrate as the paratype of *Eokotosokum bicystosum*, × 20; 13B, irregularly-arranged autozooids, × 60; 13C, two autozooids showing numerous small spine bases around the opesiae, × 127. Fig. 14, USNM 263780, Maastrichtian, Fox Hills Sandstone, Timber Lake Member; locality 3 of Cuffey *et al.* (1981), Emmons County, North Dakota. Scanning electron micrographs of coated holotype specimen imaged using back-scattered electrons; compare with Fig. 13B, × 60.

REMARKS. Gordon (1989) erected *Villicharixa* to accommodate some austral Quaternary electrid species resembling *Spinicharixa* Taylor, 1986*b*, in having numerous spines surrounding the opesia but lacking pore chambers. Unfortunately, the early astogeny of the type species of *Villicharixa* is not known. Gordon additionally referred *Electra pilosissima* Moyano to *Villicharixa*, and a third species, *Electra ongleyi* Brown (Fig. 15), also appears to belong to this genus. The assignment herein to *Villicharixa* of *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable, 1981 from the Maastrichtian of North America not only extends considerably the geological and geographical range of the genus, but also provides the first details of early astogeny in the genus.

Villicharixa lintonensis *(Cuffey, Feldmann & Pohlable, 1981)*

Figs 13–14

1981 *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable: 404–408; text-fig. 3A–C; pl. 1, figs 1–2.

MATERIAL. ROM 5337.ct.(b); Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian), locality HS, near Drumheller, Alberta; J.O.G. Sanderson Collection. A colony partially overgrown by the paratype of *Eokotosokum bicystosum*.

DESCRIPTION. Colonies are encrusting, sheet-like (Fig. 13A), multiserial and unilamellar, the zooids rather irregularly arranged (Fig. 13B). Early growth stages are not observable in the Drumheller specimen (but see Remarks).

Autozooids have an elongate ovoidal or subrhomboidal outline shape, about 1·7 times as long as wide (Table 2). One abnormally broad autozooid may be a 'doppelzooid' (Jebram & Voigt, 1977) formed by bud fusion. The opesia is ovoidal, longer than wide, and occupies about half of the frontal length of the zooid. Numerous small spine bases surround the opesia (Fig. 13C). Incomplete preservation prohibits their exact number from being counted, but there may be up to 16, the most distal pair being especially prominent. Cryptocysts are absent. The gymnocyst is well developed, particularly proximally. Laterally and distally of the opesia, it forms a steeply sloping border descending into the furrow between zooids. A broad gymnocystal tubercle may be present on the proximal edge of the opesia.

Ovicells, kenozooids and avicularia have not been observed.

Table 2 Zooidal dimensions (mm) in *Villicharixa lintonensis* (Cuffey, Feldmann & Pohlable), ROM 5337.ct.(b). Figures in parenthesis are measurements taken from the holotype specimen, USNM 263780 (Fox Hills Sandstone, North Dakota). Abbreviations as in Table 1.

	$\bar{x}$	r	SD	CV	N
zooidal length	0·494	0·44–0·56	0·038	7·6	10
	(0·533)	(0·50–0·57)	(0·028)	(5·2)	(10)
zooidal width	0·291	0·24–0·35	0·035	12·2	10
	(0·287)	(0·24–0·35)	(0·038)	(13·1)	(10)
opesial length	0·254	0·21–0·30	0·025	9·8	10
	(0·272)	(0·23–0·32)	(0·025)	(9·2)	(10)
opesial width	0·177	0·14–0·20	0·018	10·4	10
	(0·183)	(0·17–0·21)	(0·017)	(9·3)	(10)

REMARKS. This species was originally described from the Maastrichtian Fox Hills Sandstone of North Dakota as *Wilbertopora? lintonensis* by Cuffey *et al.* (1981). The type material of *V. lintonensis* (holotype = USNM 263780; paratypes = USNM 263781–3) has been re-examined using the SEM (Fig. 14), and no significant differences can be detected between it and the specimen from Drumheller. However, the following additions and amendments must be made to the original description of *V. lintonensis*:

1. The small spine bases clearly seen in the Drumheller specimen were not noted in the original description of *V. lintonensis*. They cannot be seen in the Fox Hills Sandstone specimens apparently because of the conditions of their preservation; the holotype specimen is covered by a ferruginous crust which would undoubtedly obscure the spine bases, and the paratypes show only the undersides of colonies.
2. Re-study of paratype specimen USNM 263781, which bears several colonies encrusting the inside of a mollusc, has revealed the ancestrula and early growth stages of *V. lintonensis*. The ancestrula is about 0·14 mm long by 0·09 mm wide, and buds four apparently periancestrular daughter zooids which rapidly establish the multiserial colony-form. The four periancestrular zooids are located one distally, one proximally and two distolaterally.
3. Zooidal dimensions have been re-measured in the holotype (Table 2) and, with the exception of zooidal width, were found to be appreciably larger than the figures quoted by Cuffey *et al.* (1981). In particular, zooidal length averages 0·53 mm rather than 0·37 mm as previously given.

The generic assignment of this species requires explanation. The absence of ovicells and avicularia, and presence of a proximal periancestrular bud, suggest that the species is a 'malacostegan' and is not therefore assignable to the ovicellate 'pseudomalacostegan' genus *Wilbertopora* (type species *W. mutabilis* Cheetham). Among 'malacostegans', the species invites comparison with *Electra* Lamouroux, *Spinicharixa* Taylor, and *Villicharixa* Gordon. The type species of *Electra* (*E. verticillata* = *E. pilosa*) has a periancestrular budding pattern identical to that found in the Maastrichtian species, may also develop spines around the opesia, and similarly lacks a pustulose cryptocyst. However, the gymnocyst in *E. pilosa* is porous, and well-developed pore chambers occur in the early zooids at least. *Spinicharixa* (type species *S. pitti* Taylor) possesses similar multiple spine bases, but the ancestrula buds only a distal periancestrular zooid and pore chambers are present. Although early astogeny is unknown in the type and other species of *Villicharixa*, assignment of the Maastrichtian species to this genus is preferred. *V. lintonensis* closely resembles *V. ongleyi* (Brown) from the ?Pleistocene of New Zealand. The holotype of *V. ongleyi* is re-illustrated here for comparative purposes (Fig. 15). *V. lintonensis* differs from *V. ongleyi* mainly in the presence of a gymnocystal tubercle on the proximal edge of the opesia, and in the poorly-developed cryptocyst, a feature shared with *V. strigosa* (Uttley).

During life the intact spines of *V. lintonensis* would probably have formed a loose, hairy covering to the frontal membrane of the zooids, as in the specimen of *V. strigosa* depicted by Gordon (1989: fig. 2A).

DISTRIBUTION. Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian); locality HS, near Drumheller, Alberta, Canada. Timber Lake and Colgate Sandstone Members, Fox Hills Sandstone

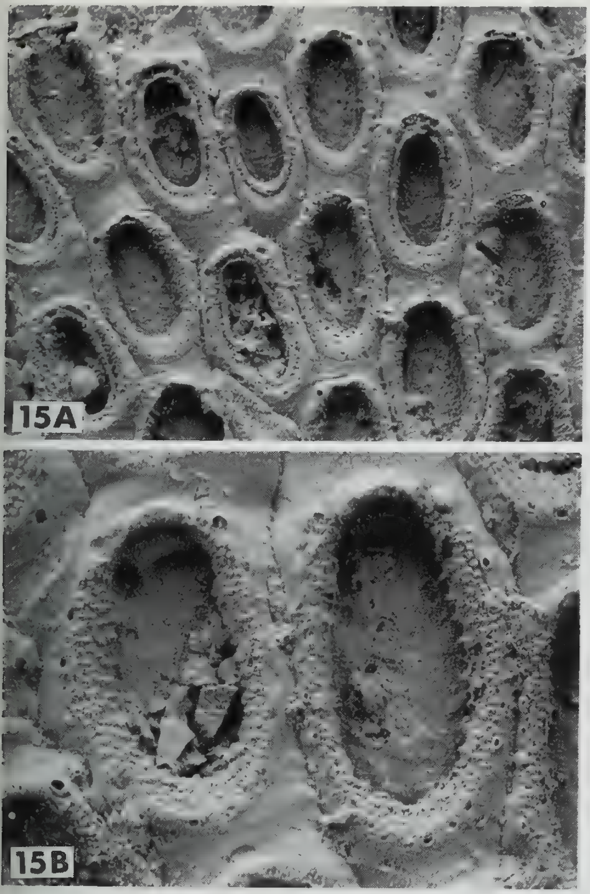


Fig. 15 *Villicharixa ongleyi* (Brown), BMNH D36532, holotype, [probably L. Pleistocene, Petane Limestone], Petane, New Zealand; compare with *V. lintonensis* (Figs 13–14). Scanning electron micrographs of uncoated specimen. 15A, autozooids, some with 'regenerations', × 54; 15B, two autozooids showing numerous small spine bases around the opesiae, × 120.

(middle Maastrichtian); localities near Linton, North Dakota, U.S.A. (Cuffey *et al.*, 1981: 401–2). It is also possible that the bryozoan listed from the Fox Hills Sandstone (lower to middle Maastrichtian) in southern Alberta (Sanderson 1931: 1254; Allan & Sanderson 1945: 79) may represent *Villicharixa lintonensis* rather than *Eokotosokum bicystosum*, as noted above (p. 21).

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Lower Devonian fishes from Saudi Arabia*

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Synopsis. Fragmentary fishes preserved in bone beds are described from the Jauf Formation and Wajid Sandstone of Saudi Arabia. They support previous opinions that the Jauf Formation represents a shallow and marginal marine deposit of Pragian age. Identification of a similar but more restricted fish fauna in the Wajid Sandstone suggests that at least part of this deposit, originally designated as 'Lower Permian and older?', should also be considered as Pragian. Two new taxa are described: *Wajidosteus minutus* gen. et sp. nov. is a small phlyctaeniid arthrodire and *Jaufolepis striata* gen. et sp. nov. is a new diplacanthid acanthodian. The fauna is compared with other Lower and Lower/Middle Devonian fish faunas. The Saudi fauna seems most similar to an Eifelian fauna from Khush Yeilagh, northern Iran, and is to be considered part of the Rhenish Bohemian faunal realm. Some notes are included on the sedimentology and palaeoenvironmental interpretation of the fish-bearing sediments.

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* This paper is part of IGCP Project 328.

INTRODUCTION

Palaeozoic rocks in the Arabian Peninsula occur extensively in the sedimentary outcrop belt of central and western Saudi Arabia, wrapped around the Arabian Precambrian shield in a north–south trending arcuate band that covers a distance of over 1500 km. Sequences of more limited extent also occur in part of Oman. The Devonian rocks, while extensively distributed in the subsurface of eastern Arabia, are of limited geographical extent at the surface since they are usually truncated at Pre-Permian and Cretaceous erosion intervals. Outcrops of Devonian rocks occur in northwest Saudi Arabia in the Jawf/Sakakah area, where they are mapped in the successively younger Tawil Sandstone, Jauf, and Jubah (Sakaka) Sandstone formations, and at a recently discovered site located far to the south in the southernmost part of the Wajid Sandstone (Jibal al Wajid) complex (Fig. 1). Devonian fishes are found in both areas. An analysis of the Devonian rocks of Saudi Arabia is given by Boucot *et al.* (1989) and surface Devonian rocks are indicated on the maps of the United States Geological Survey (Bramkamp *et al.* 1963*a*, *b*) and on maps of the Saudi Arabian Ministry of Petroleum and Minerals (Meissner *et al.* 1986, 1989). Original description and definition of Devonian rock units are found in Powers *et al.* (1966) and Powers (1968). Boucot *et al.* (1989) presented a study of the palaeontology, biostratigraphy and biogeography of the Devonian of Saudi Arabia, which concentrated on the outcrop of the Jauf Formation. The basis for that study was fossils collected by one of us (H.A.M.) and others of the Arabian American Oil Company (now Saudi Aramco) in 1987–8.

The Devonian rocks containing the fishes are sandstones, shales and occasional limestones which were deposited on a broad, tectonically stable epicontinental shelf, the Arabian platform. Depositional environments of the Devonian range from continental to shallow marine. The Jauf Formation is approximately 300 m thick at the type locality and is composed of shale, limestones and minor sandstones, which together with the fossils suggest environments ranging from fluvial and flood plain to marine. The overlying Jubah Sandstone is largely continental. Marine transgressions and regressions caused by eustatic changes occur throughout the Jauf Formation (Fig. 2). The fossils from the Jauf Formation date this deposit as Pragian to early Emsian, while the underlying Tawil Sandstone is dated as early Devonian on the basis of brachiopods (Boucot *et al.*, 1989). The immediately overlying and conformable Jubah Sandstone is considered Emsian.

OCCURENCE OF FOSSIL FISHES AND PLANTS AND DEPOSITIONAL ENVIRONMENTS

Palaeozoic fishes from the Devonian of the Arabian Peninsula are very poorly known. Powers *et al.* (1966) listed dermal scutes of fishes as occurring in the Jauf Formation. Bahafzallah *et al.* (1981) mentioned the occurrence of fish remains in the Jauf. An arctolepid plate was described from a Devonian borehole sample from Qatar (White 1969). Turner (*in* Boucot *et al.* 1989) described acanthodian and placoderm scales from the Jauf Formation and Lelièvre (1989) described a head plate of a buchanosteid arthrodire. The fossil fishes described in this paper come from 12 selected sample localities: one in the Wajid Sandstone, nine in the Jauf Formation and two in the Jubah Sandstone. Other fish-bearing beds occur in the section but fossil specimens are rare or too badly preserved to warrant analysis.

Fish remains in the Jauf Formation and Jubah Sandstone appear to occur in three contexts which probably represent different depositional environments (Fig. 3). These are: (1) coarse to medium-grained and poorly sorted sandstone often with rip up clasts and channel features, probably of continental flood plain and fluvial nature where fish are most common and with no marine fossils (except very rare lingulids); (2) claystone, where the other fossils associated with the fishes are mostly small lingulids, an environment which possibly represents deposition in mud lagoons with very brackish water, or perhaps estuarine ponds; (3) limestones containing brachiopods, trilobites, corals and molluscs and which represent shallow water marine conditions in which fish fossils are very rare.

The depositional environments of the Jauf Formation are discussed in more detail in Boucot *et al.* (1989) and the probable specific environments of each of the samples studied in this paper are given in the Appendix (p. 41). A remarkable feature of the formation is the rapid and extremely brief sea-level fluctuations recorded in the section (Fig. 2).

Fossil fishes and plants from the Wajid Sandstone occur in very silty, well indurated, varicoloured micaceous claystone with indistinct irregular bedding and discrete 'floating' fine sand grains. Of limited geographic extent and only 1.5 m thick, the unit either lies directly on basement complex, or is unconformably separated from the basement by a thin, well sorted, medium grained sandstone. This basal sandstone, where present, varies rapidly in thickness but is uniform in texture and mineral content. This suggests that it developed as a discontinuous deposit marginal to a large water body and that it probably infilled local topographic lows in the basement terrain. The excellent sorting and low angle to planar crossbedding suggests that it was not of fluvial origin. A low energy, quiet water environment is indicated by the claystone containing the fishes and the discretely scattered sand grains may indicate transportation by wind. Frequent small clusters and string-like occurrences of sand grains may be faecal in origin. The claystone is overlain by a distinct desiccation horizon and then partly by a geographically extensive sandstone which is thick, coarse-grained, and massively bedded with some cross bedding. This is the more typical Wajid Sandstone facies which probably represents deposition in extensive flood plain and fluvial environments. The fish- and plantbearing claystone is interpreted as having been deposited in a highly restricted quiet water basin, possibly a cut off lagoon (or perhaps a lake). No other fossils are present to aid interpretation of the environment. The underlying sandstone may represent a shoreline facies, where both aqueous and aeolian processes enhanced the sediment maturity. Eventually the basin filled in and severe desiccation followed, prior to the final inundation by coarse, fluvially-transported sands of the massive Wajid Sandstone. The claystone unit was not previously recognized and so no fossils were thought to occur in the Wajid Formation; hence the previous dating as 'Lower Permian and older' (Powers *et al.* 1966 ; Powers 1968). The contained Devonian fishes described in this paper suggest that at least the basal claystone unit is Devonian anc

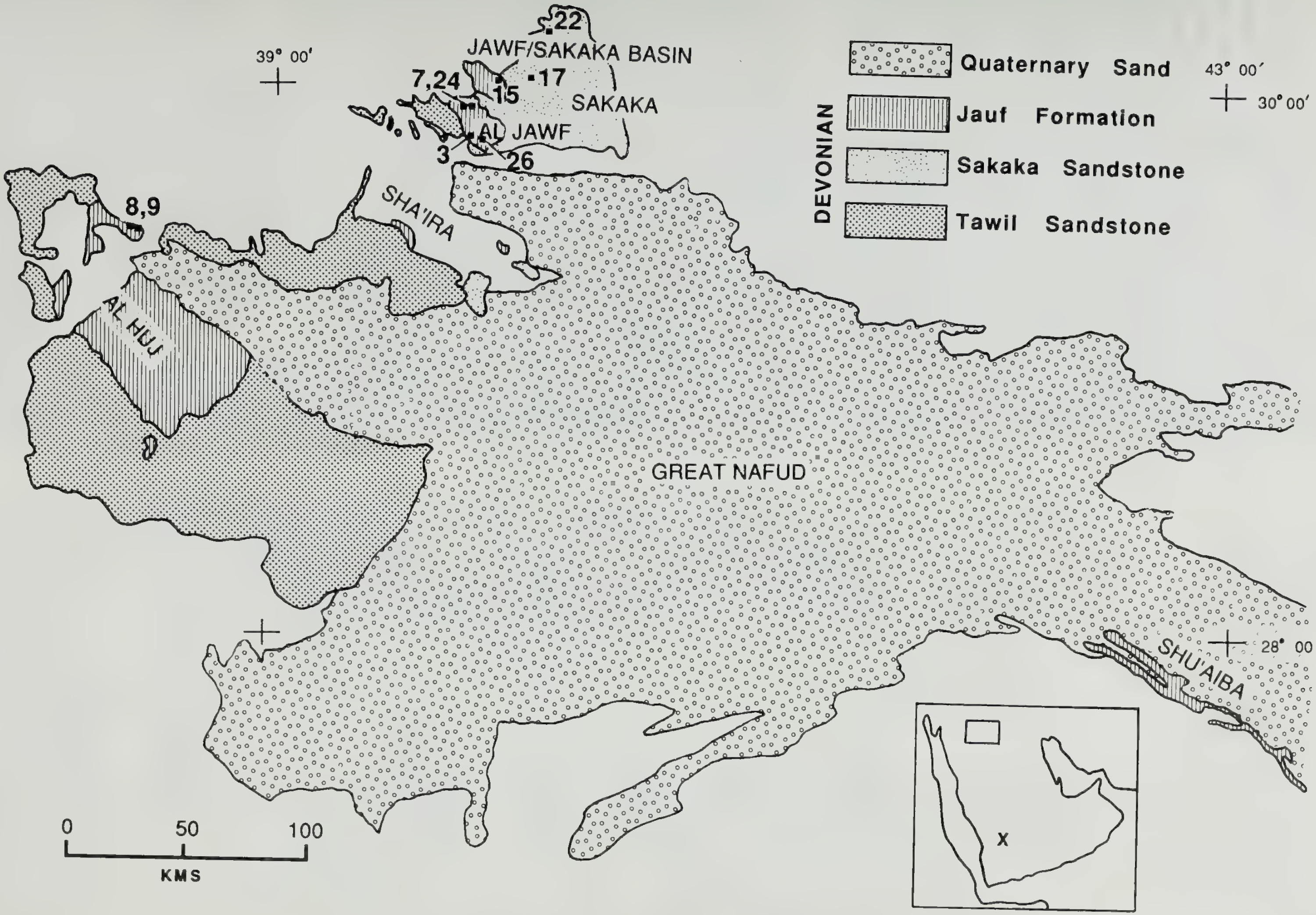

39° 00′
43° 00′
30° 00′
28° 00
22
JAWF/SAKAKA BASIN
7,24
15
17
SAKAKA
AL JAWF
3
26
8,9
SHA'IRA
AL HIJJ
GREAT NAFUD
SHU'AIBA
DEVONIAN
Quaternary Sand
Jauf Formation
Sakaka Sandstone
Tawil Sandstone
0
50
100
KMS
X

Fig. 1 Map showing the Devonian outcrop area in Saudi Arabia. The localities in the Jauf Formation are numbered to correspond with those used throughout this paper. The Wajid Sandstone locality in the south of the country is shown only in the inset map, indicated by **X**. The Wajid Sandstone is part of a sequence as yet unmapped. [Modified after Boucot *et al.* 1989.]

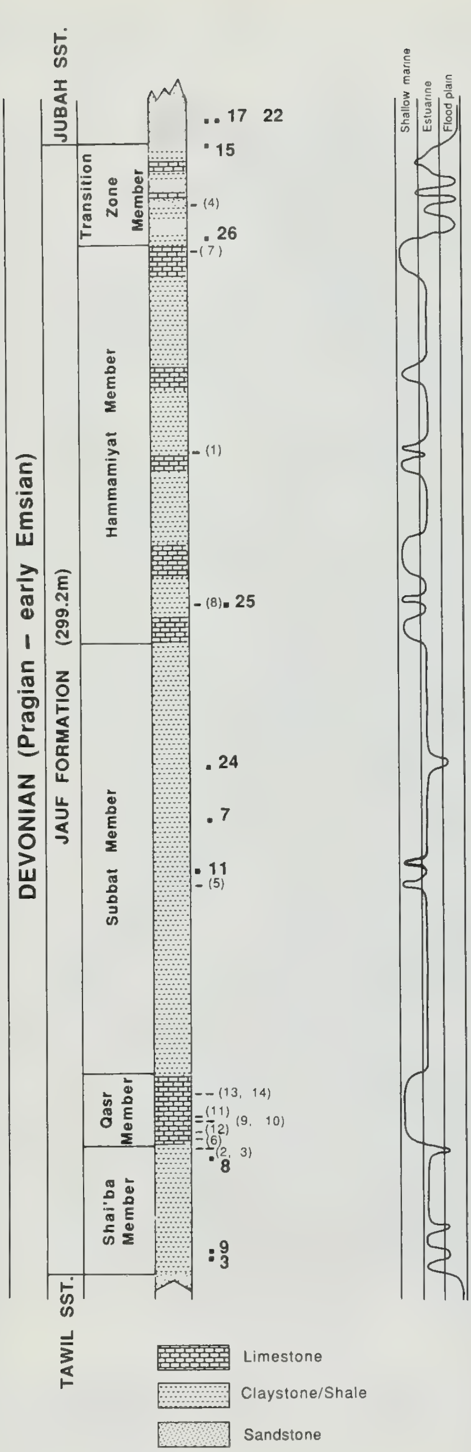


Fig. 2 Generalized stratigraphic section of the Jauf Formation. The lithologies shown are general; for detailed descriptions of the sampled parts of the section see the Appendix. The position of the sample numbers are shown with those examined and numbered by Boucot *et al.* (1989) given in parentheses. On the whole Boucot *et al.* sampled the more truly marine levels. The transgressive/regressive curve to the right is based upon evaluation of several parameters: lithology, fossil content from all available samples, lithology/fossil associations, fossil/fossil associations, and sedimentary features.

contemporaneous with the Subbat Shale Member of the Jauf Formation. The few small plant fragments in the Wajid cannot be usefully identified.

The Jubah Sandstone (see Meissner *et al.*, 1989 for definition) is largely of continental origin. The only fossil known, except for the fishes described here, is a herbaceous lycophyte similar to *Haskinsia* or *Colpodexylon*, which occur in Middle and Upper Devonian rocks in Laurentia. While most of the Jubah Sandstone may be considered continental in origin, the occurrence of a single lingulid brachiopod together with the fishes in Sample 22 (see Appendix, p. 42) may serve to indicate a very brief marginal marine or estuarine phase near the base of the sequence. The other Sample (17, p. 42) appears to represent a shallow stream deposit, perhaps laid down in a braided flood plain. The overall sedimentary evidence and fossil associations documented (stream or flood plain or outwash deposits) probably indicates a fresh-water aspect to most of the fish beds studied here, although there was possibly some brackish water incursions due to backflooding in an estuarine situation. Sample 22 (p. 42) contains only one lingulid specimen in what otherwise appears to be fluvial outwash deposit, which might mean that the marine back flooding was only due to an exceptional storm tide.

SYSTEMATIC PALAEONTOLOGY

In this section the fishes from both the Jauf Formation and the Wajid Sandstone are described. Some taxa are common to both. In many cases the specimens are broken, meaning that photographs are less useful than the drawings which combine information from more than one specimen. Where sample numbers are given these refer to those cited in the Appendix and plotted on the section (Fig. 2). All specimens referred to by register number are in the collections of the Department of Palaeontology, Natural History Museum.

Abbreviations. The following abbreviations are used in the descriptions of the fishes: ADL, anterior dorso-lateral plate; AMV, anterior medio-ventral plate; AL, anterior lateral plate; AV; antero-ventral plate; AVL anterior ventro-lateral plate; IL, intero-lateral plate; MD, median dorsal plate; PDL posterior dorso-lateral plate; PMV, posterior medio-ventral plate; SP, spinal plate.

Subclass **PLACODERMI**
Order **ARTHRODIRA**
Suborder **PHLYCTAENOIDEI**
Infraorder **PHLYCTAENII**
Phlyctaenii incertae sedis

Genus ***WAJIDOSTEUS*** nov.

DIAGNOSIS. Very small phlyctaenioid arthrodire measuring an estimated 14 mm across the ventral trunk shield at the level of the interolaterals. The ventral shield is longer than wide. Spinals are stout, reaching just beyond the posterior level of the AVL and bearing about 20 small medial denticles. Trunk shield tall, with both AL and ADL being deeper than long. ADL with small trochlear. Overlap surface on ADL for the MD (unknown) is sinuous. Ornament consists of many fine tubercles, regularly spaced.

NAME. After the Wajid Sandstone, the formation in which the holotype was found.

Wajidosteus minutus sp. nov. Figs 4, 5, 21, 22

DIAGNOSIS. As for genus, only species.

HOLOTYPE. P62836a, b ADL in part and counterpart, Wajid Sandstone, 17°36′N 44°5.5′E.

MATERIAL. P62826 (AL), P62827 (left AVL, SP), P62828 (left IL, SP, AVL), P62829 (left AVL, SP), P62830 (crushed trunk shield with a few trunk scales), P62831 (left IL, SP, AVL), P62832 (left AVL, SP), P62833a, b (AL), P62834a, b (right IL, SP+AVL), P62835a, b (AL): all from Wajid Sandstone. Specimen P62865 from sample 3, Jauf Formation, is the impression of an AVL.

DESCRIPTION. This species is known only from a few isolated trunk plates and a badly crushed shield with scales. Association of individual plates is suggested by the similarity in ornament and congruent size. Even though the specimens are very small it is probable that they represent adult growth stages because the sutures between IL, SP and AVL are obscured and these elements tend to hold together in the few available specimens. Using the synapomorphy scheme proposed by Goujet (1984) *Wajidosteus* is recognized as a phlyctaenioid by the presence of a trochlear, implying a ball and socket neck joint, and the absence of an AV plate (synapomorphy of actinolepidoids). It is suggested that it is a phlyctaeniid because the spinal plates are relatively strongly developed but, within this assemblage of about 15 genera, comparisons become imprecise. One unusual feature of *Wajidosteus* is that both the AL and ADL are restored as being deep (Fig. 5). Amongst phlyctaeniids this is seen in the monotypic forms such as *Tiaraspis* Gross 1962, *Kolpaspis* Pageau 1969, *Gaspeaspis* Pageau 1969 and *Aggeraspis* Gross 1962. The overall size of this placoderm is most like that of *Huginaspis* or *Gaspeaspis*, as is the posterodorsal process upon the AL (Pageau 1969: pl. 33, fig. 7B). The ADL is the most distinctive of the known elements and a specimen of this is chosen as the holotype. It resembles that of *Tiaraspis* in that the dorsal overlap surface is sigmoidal (in most phlyctaeniids it is straight). The lateral line is deeply incised along the middle of the ADL and there is an accessory twig of the lateral line. However, unlike *Tiaraspis* and *Groenlandaspis* Heintz 1932 there is no evidence that the ADL's of either side met one another beneath the MD (unknown in *Wajidosteus*). The AMV is badly preserved in specimen P62828 but it seems to be short and broad and triangular implying that there was little or no contact with the PMV. The ornament is developed as tiny tubercles, regularly arranged and distributed evenly; it becomes coarser at the level of the trochlear on the ADL and along the outer margin of the spinal. In all, the shape of the trunk shield and the ornament most closely resembles that illustrated for *Huginaspis* by Heintz (1929: pl. 3), differing mainly in the slightly longer spinals and the presence of an accessory twig of the lateral line.

cf. *Elegantaspis* Heintz 1929 Fig. 6

The present collection contains one specimen from the Wajid Sandstone (P62837: a trunk shield, parts of head plates and a few scales). Virtually no detail may be seen and comparisons with other placoderms can only be on the most superficial level and is restricted to overall shape. This specimen is considered to be a phlyctaeniid because of the long narrow trunk shield and the long spinal. Like *Wajidosteus* it is a very small placoderm, the trunk shield measures 22 mm long. The spinal is long; although incomplete it was probably longer than the trunk shield, and is straight without medial tubercles. These features are very similar to those of *Elegantaspis recticornis*, a species described from the Siegenian Wood Bay Series of Spitzbergen (Heintz 1929).

Order **PETALICHTHYIDA**

Gen. et sp. indet. Fig. 23

Several specimens within samples 3 and 11, Jauf Formation, may be compared to petalichthyid placoderms but the comparison is based mainly on similarities in the pattern of ornamentation and identification must remain tentative until more complete specimens are found. Specimen P62863a, b appears to be part of a head shield and, to judge from the patterns of ornament, there are parts of three plates represented. It is not possible to identify the plates. The ornament consists of smooth tubercles which are arranged in groups of two, three or four at the presumed centre of ossification and then they are arranged in radiating rows towards the margins of the plates. P62949 (sample 11) is an ADL showing well the prominent lateral line developed as a series of pores. Specimens P62862, P62950 (sample 11) and P62863a, b show small portions of spinal plates with similar ornament. In these spinals the tubercles of ornament are aligned along about seven clearly defined rows. The tubercles are closely spaced and are of constant size, and are slightly flattened from side to side and also slightly asymmetrical so that the tips tilt towards the distal end. The leading edge of the spinal is ornamented with slightly enlarged tubercles while the trailing edge bears prominent denticles angled towards the base of the spinal. This type of ornament is identical to that found in petalichthyids, and of all petalichthyids the Saudi specimens resemble *Wijdeaspis* most closely. This is a genus with species found in the Eifelian of Spitzbergen (*W. arctica* (Heintz 1929)), Emsian of New South Wales (*W. waroonensis* Young 1978) and Eifelian of Severnaya Zemlya , Taimyr and the Siberian platform (*Wijdeaspis* sp. (Obruchev 1967)). From the Wajid Sandstone there is a single specimen (P62838) representing a nuchal plate probably referable to a petalichthyid. The plate is very elongate and each lateral margin is embayed as three shallow excavations marking the contact edges with anterior and posterior paranuchals, centrals and preorbitals. The shape of this nuchal matches that seen in petalichthyids such as *Wijdeaspis*, *Notopetalichthys* (Emsian of New South Wales), *Shearsbeaspis* (Emsian of New South Wales) and *Lunaspis* (Siegenian–Emsian of Germany, Emsian of New South Wales and the Lower Devonian of China).

Other placoderms

Amongst the collection from the Wajid Sandstone there are several specimens of larger placoderms which cannot be associated with each other, nor can they be closely identified. Two of these can reasonably be phlyctaeniids. P62843 is a long shallow PDL, 30 mm long and 10 mm high; it is rectangular, very similar in shape to that figured for *Dicksonosteus*

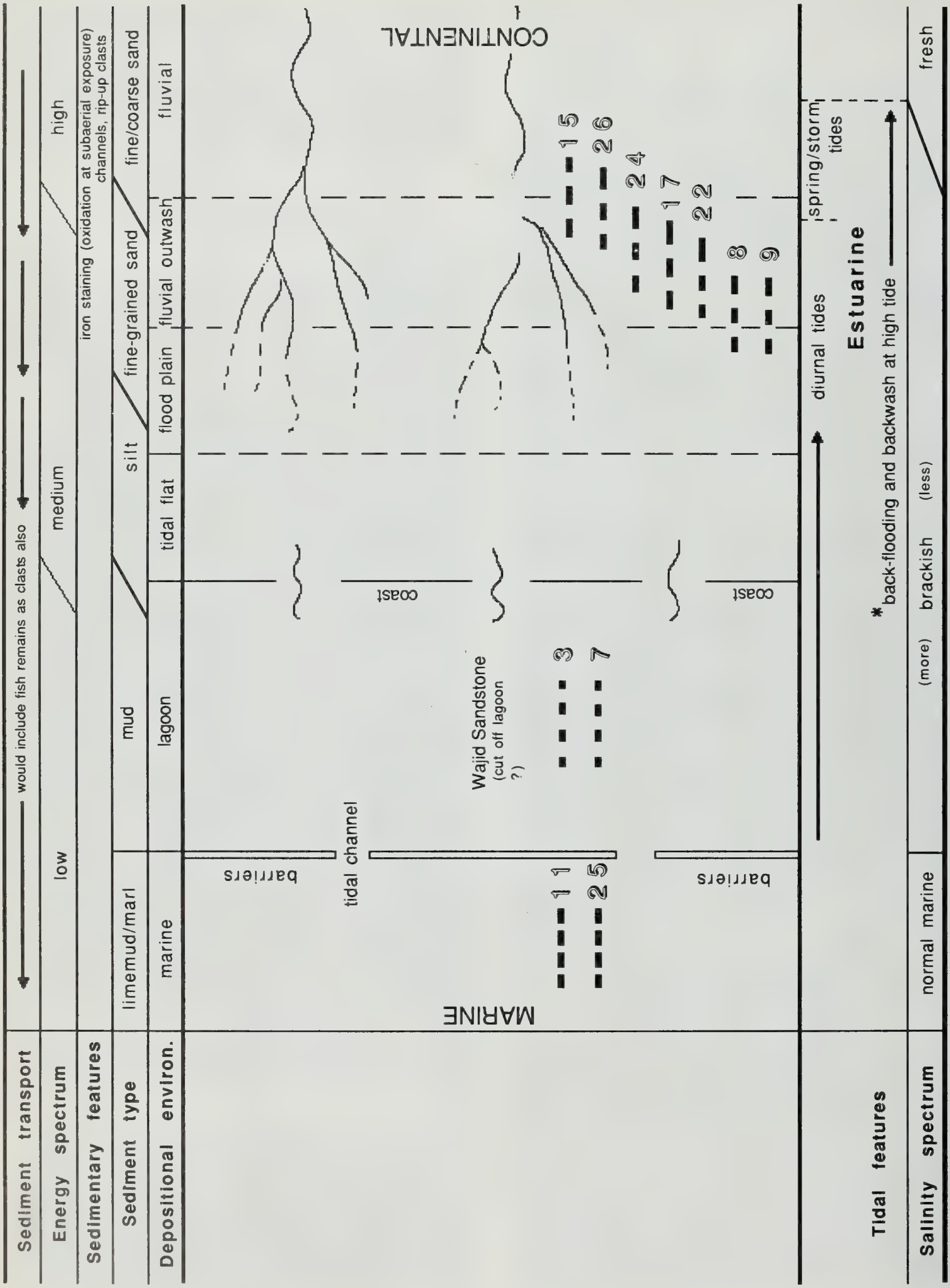
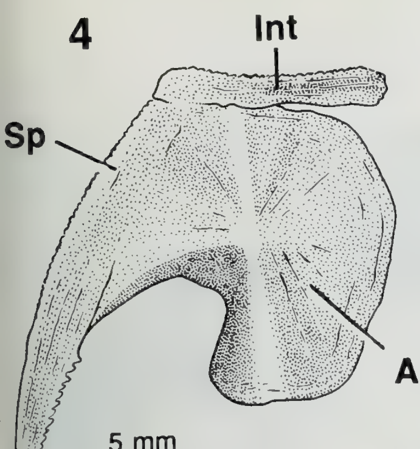
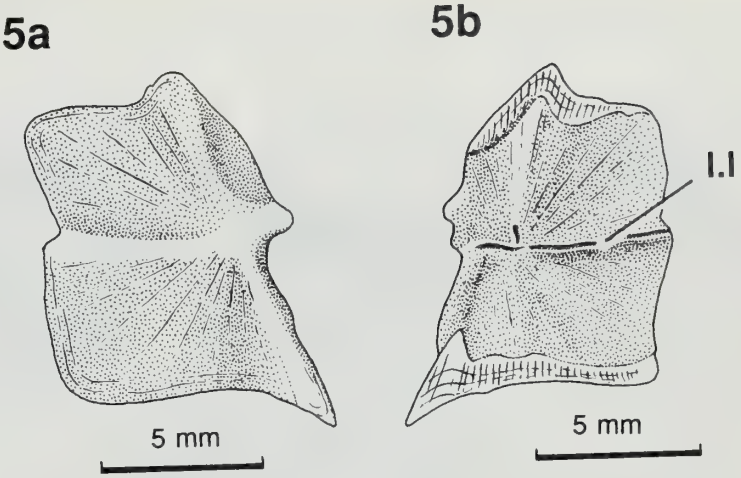
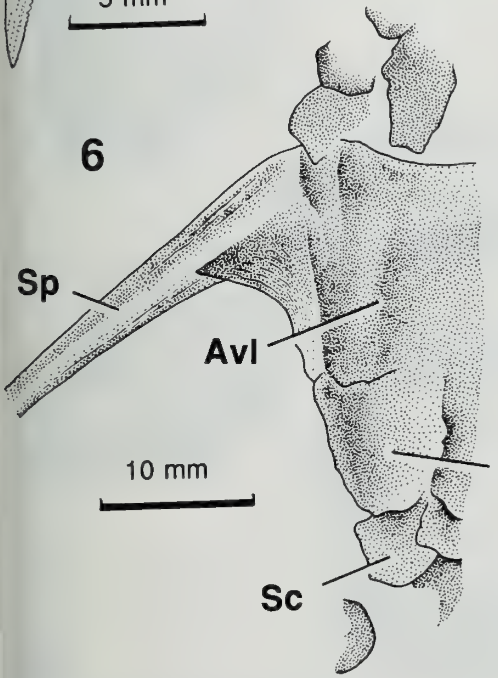
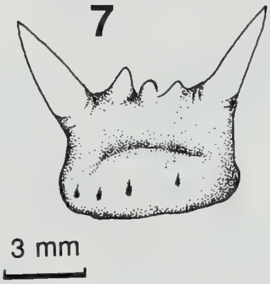

Sediment transport
would include fish remains as clasts also
Energy spectrum
low
medium
high
Sedimentary features
iron staining (oxidation at subaerial exposure) channels, rip-up clasts
Sediment type
limemud/marl
mud
silt
fine-grained sand
fine/coarse sand
Depositional environ.
marine
lagoon
tidal flat
flood plain
fluvial outwash
fluvial
MARINE
barriers
tidal channel
barriers
11
25
Wajid Sandstone (cut off lagoon ?)
3
7
coast
coast
CONTINENTAL
15
26
24
17
22
8
9
Tidal features
diurnal tides
spring/storm tides
Estuarine
*back-flooding and backwash at high tide
Salinity spectrum
normal marine
(more)
brackish
(less)
fresh

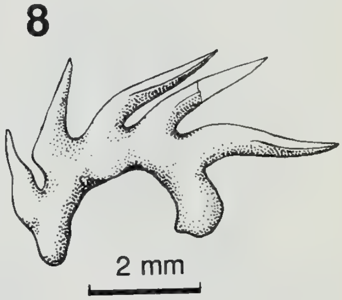
Fig. 3 Environmental and sedimentological scenario of the fish-bearing localities in the Jauf Formation and Wajid Sandstone, based on sedimentological and palaeontological evidence.

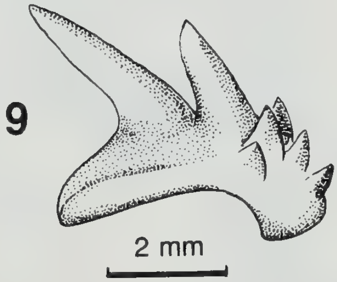












Figs 4–5 *Wajidosteus minutus* gen. et sp. nov. 4, ventral view of part of ventral trunk armour, based on P62831. Sp – spinal, Int – intero-lateral, Avl – anterior ventrolateral. 5, Anterior dorso-lateral ; a inner, b outer views. **Holotype** P62836a, b. l.l – lateral line groove. (See also Fig. 22).

Fig. 6 cf. *Elegantaspis*. Ventral trunk armour, scattered head plate and scales. P62837. Sp – spinal, Avl – anterior ventro-lateral, Pvl – posterior ventrolateral, Sc – scale.

Fig. 7 *Phoebodus* sp. tooth P62874, tips of lateral cusps restored.

Fig. 8 Ischnacanthid symphysial tooth whorl. P62867.

Fig. 9 cf. *Onychodus anglicus* Woodward. Tooth whorl. P62853.

y Goujet (1984: fig. 63). Others (P62839 and P62840) are Ls, 18 mm and 22 mm deep but otherwise similar in shape o those of *Wajidosteus*. Two further specimens are long, offin-shaped AMVs (P62842, P62846a, b), much narrower han those seen in *Wajidosteus*. P62845a, b and P62848 are imilar shaped AVL plates, 22 mm and 34 mm long respectively and the spinal margin shows that the placoderm to vhich they belonged had very divergent spinals. P62841 is lso an AVL showing a divergent spinal margin but it is lightly more elongate. Lelièvre (1989) described the central late of a buchanosteid arthrodire from the Jauf Formation. here are plates with buchanosteid type ornament pattern in the present collection although we have been unable to identify them further.

Turner (*in* Boucot *et al.* 1989) recorded the occurrence of placoderm scales within a sample from the Jauf Formation and compared them with those of *Stensioella*. We have recovered more such scales from sample number 17 (P62958–60) and they are illustrated in Figs 16–18. Generally the scales are small, conical with a rough uneven surface of ridges, depressions and sometimes tubercles. The lower surface is deeply concave. Some are similar to those identified by Turner, others resemble scales attributed to *Asterosteus*, an

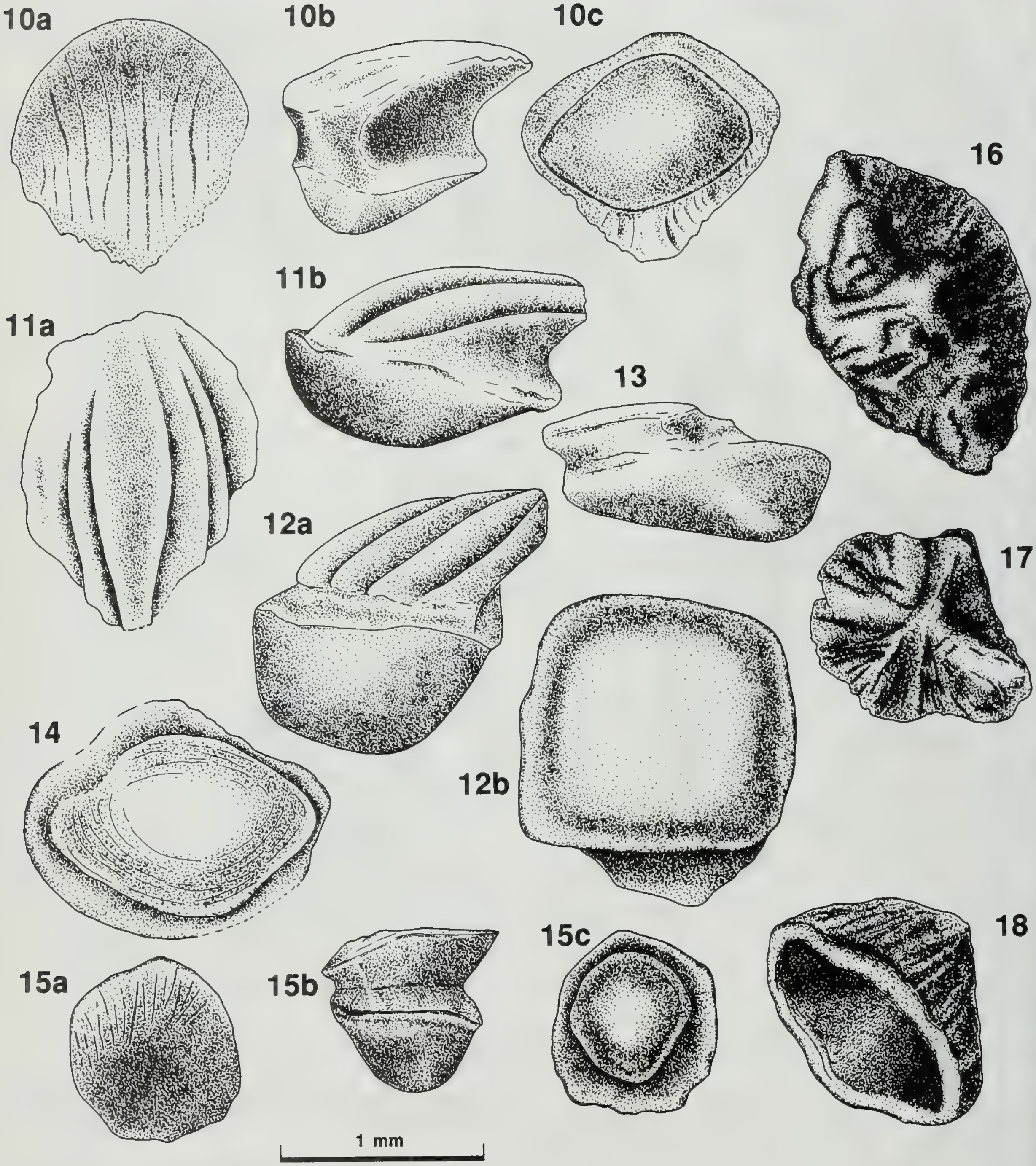


Fig. 10 Diplacanthid scale. a crown, b lateral, c basal views. P62951.

Fig. 11–14 *Nostolepis striata* Pander. 11, scale; a crown, b lateral views. P62954. 12, scale; a lateral, b basal views. P62952. 13, scale, lateral view. P62956. 14, scale, basal view. P62955.

Fig. 15 *Cheiracanthoides* cf. *comptus* Wells. Scale; a crown, b lateral, c basal views. P62953.

Figs 16–18 Three types of placoderms scales. 16, crown view P62958. 17, crown view P62959. 18, basal view P62960.

All figures to same scale. Scale bar applies to all.

Upper Devonian rhenanid (cf. Denison 1978: fig. 13).

Subclass **ACANTHODII**

The acanthodians are represented mostly as disarticulated scales and spines and this is not uncommon in many other Lower Devonian localities. The state of acanthodian taxonomy reflects this and many taxa are erected for either scales or spines. Because of this the scales are here treated separately from the spines.

Order **CLIMATIIDA**

Family **CLIMATIIDAE** Berg 1940 [scales]

Genus ***NOSTOLEPIS*** Pander 1856

Nostolepis striata Pander 1856 Figs 11–14

Material. Scales from the Jauf Formation samples 3, 9, 17 (P62956), 22, 15 (P62954), 26 (P62952).

Remarks. These scales have a deep, narrow crown which overhangs the base posteriorly, and is produced to a point. The neck is rhombic and hardly distinct as it passes from the crown into a deep, strongly convex base which often shows growth lines. The degree of convexity varies from scale to scale, and may reflect different growth stages and/or different sites of origin over the body. The surface ornament consists of several paired, pronounced, symmetrically arranged ridges, the central pair bordering a median boatshaped depression and converging posteriorly to form a point. The overall shape and histology of these scales are similar to those of climatiid scales. In that they have posteriorly converging ridges these scales are similar to *Nostolepis striata* as described by Wang & Dong (1989), *N. sinica* Gagnier, Janke & Shi 1989*a* and *N. costata* Goujet 1976, and to scales described by Giffin (1980) as *Cheiracanthoides comptus*. They differ from *N. sinica* in lacking serrated edges, and from Giffin's scales in lacking a median ornament ridge in the crown. Scales of *N. costata* were identified by Turner (*in* Boucot *et al.* 1989) from the Jauf Formation. The scales described here show the ornament ridges set at an angle, facing laterally, and in this respect they are most similar to scales described as *N. striata* by Wang & Dong (1989) and by Gross (1947). *N. striata* is elsewhere discussed by Novitskaya & Obruchev (1967) and by Pander (1856).

Cheiracanthoides cf. ***comptus*** Wells 1944 Figs 15 a–c

Material. Scales from samples 22 (P62955), 15 (P62953), Jauf Formation.

Remarks. Turner (*in* Boucot *et al.* 1989) had identified scales of *Cheiracanthoides comptus* within the Jauf Formation. Each of the scales we have identified shows a crown which is relatively flat-topped with only a slight bevel along the curved anterior margin. The gently curved anterior and posterior margins of the crown barely overhang the base, from which it is separated by a narrow and deeply incised neck. The base is deep, convex and shows obvious growth lines. The ornament consists of wide, shallow ridges irregularly arranged and separated by narrow grooves. The ridges converge slightly posteriorly where they become indistinct and therefore do not cover the entire crown. These scales are very similar to the *Cheiracanthoides comptus* scales described by Wells (1944: fig. 4a–c).

Family **DIPLACANTHIDAE** Woodward 1891

Gen. et sp. indet. Fig. 10

Material. Scales from the Jauf Formation, samples 17, 22, 15, 26 (P62951). The crown is almost flat topped to gently convex. The anterior margin of the crown is curved in an arc. Low ridges run longitudinally from the anterior to the posterior margins of the crown, and are almost parallel to each other, diverging slightly anterolaterally. Posteriorly the margins of the crown converge to form a medial point. Posterolaterally the margins of the crown are sculptured to form an irregularly serrated margin. The posterior margin of the crown extends beyond the margin of the base, and the base is not visible from above in plan view. The anterior margins of the crown and base are approximately level. The neck is wide and forms a distinct division between the crown and the base. Towards the anterior the base is convex and quite deep. Its surface often shows parallel horizontal growth lines. The scales of this type from Saudi Arabia show a strong resemblance to scales of Givetian age from Antarctica (G.C. Young, personal communication and 1989: fig. 4C).

Genus ***JAUFOLEPIS*** nov.

Diagnosis. Based on a patch of scales showing shallow bases and crowns of two sorts. Smaller scales have closely serrated posterior margins and a crown marked by faint longitudinal ridges towards the posterior margin. Larger scales have large, elongate crowns extending well beyond the base and ornamented with irregular ridges curving inwards posteriorly and becoming indistinct.

Name. After the Jauf Formation.

Jaufolepis striata gen. et sp. nov. Figs 19, 24

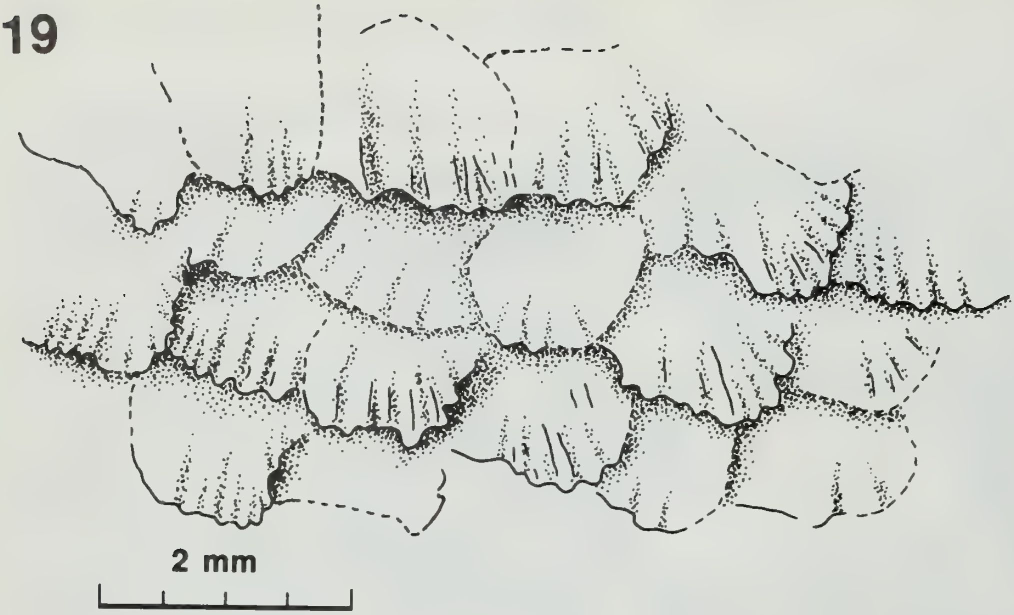
Diagnosis. As for genus, the only species.

Holotype. P62957a, b, impressions of two kinds of scales from sample 24, Jauf Formation.

Description. The patch of scales contains two kinds of scale which very clearly belong to the same fish and no doubt grade into one another. Since only the bases of most of the scales are exposed it is not possible to determine the extent of this gradation. All the bases are shallow. Scales of the smaller type have a gently convex crown which extends posteriorly beyond the base. The posterior margins of the crown are serrated and the evidence of former growth stages is present as a delicate scalloped patterning. The surface of the crown is marked by faint longitudinal ridges towards the posterior margin. The anterior part of the crown was not seen. The larger scales have large, elongate crowns which extend a considerable way beyond the base. The surface is ornamented with faint ridges which curve inwards posteriorly to become indistinct. The posterior margin of the large scales is generally not well preserved but seems to taper to a point. The posterior outline seems to vary among scales but this may be an artifact.

The marked variation in scale types seen in P62957a, b is

19



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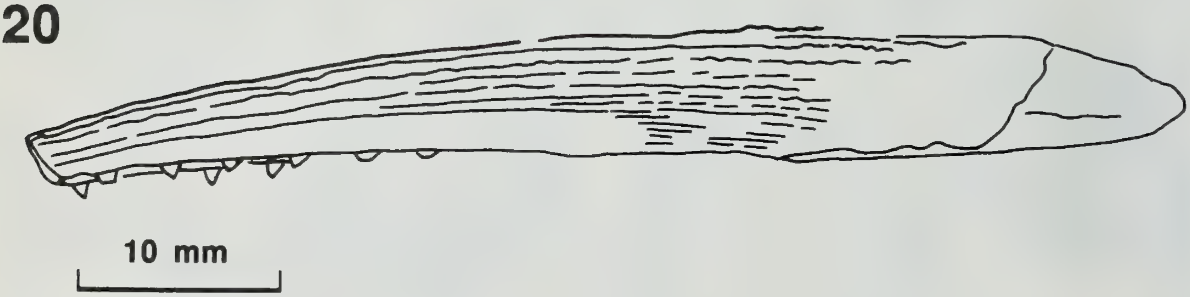

Fig. 19 *Jaufolepis striata* gen. et sp. nov. Group of small scales. **Holotype** P62957b. (See also Fig. 24).
Fig. 20 *Parexus* sp. Spine showing typical alternating arrangement of posterior denticles. P62870. (See also Fig. 25).

not seen in many other acanthodians. It is associated with the Diplacanthidae by virtue of the scalloped patterning within the crown and the surface ornament of longitudinal ridges, although the ridges are indistinct on the smaller scales.

Family **CLIMATIIDAE** Berg 1940 [spines]

Genus *Parexus* Agassiz 1845

Parexus **sp.** Figs 20, 25

MATERIAL. One almost complete spine, P62870 from sample 8.

REMARKS. This is a slender spine with long narrow ridges running parallel to the axis and a short insertion area. Basally there are eight ridges but some fade out so that there are only four at the tip. The proximal ends of the ridges bear noded ornament. The spine is gently curved and slightly flattened from side to side; this latter feature is unlike the straight spines of *Parexus*. However, as in species of *Parexus* there are denticles arranged in alternate fashion at the distal end of the trailing edge.

Climatiidae *incertae sedis*

MATERIAL. Two fin spines P62857 and P62858. Both specimens are from sample 9 from the Jauf Formation.

Specimen P62858 is a portion, 62 mm in length, of a fin

Figs 21–22 *Wajidosteus minutus* gen. et sp. nov. 21, ventral view of part of ventral trunk armour. P62828 (cast). 22, ADL, cast of outer view. **Holotype** P62836b. (See also Fig. 5).
Fig. 23 Petalichthyid spine, Gen. et sp. indet. P62862.
Fig. 24 *Jaufolepis striata* gen. et sp. nov. a, group of small scales. b, two of the larger scales. **Holotype** P62957a, b.
Fig. 25 *Parexus* sp. Spine P62870 (cast). (See also Fig. 20).
Figs 26–27 *Uraniacanthus spinosus* Miles. 26, P62861 (cast). 27, spine P62860 (cast).
Fig. 28 cf. *Gyracanthus incurvus* Traquair. Spine P62814a (cast).

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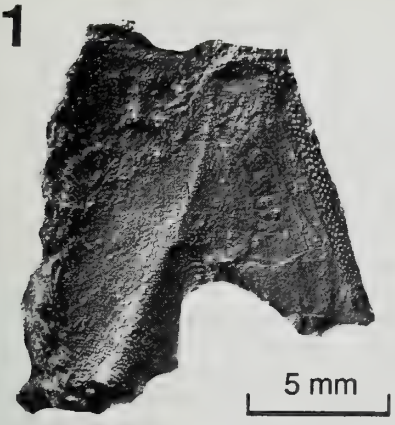

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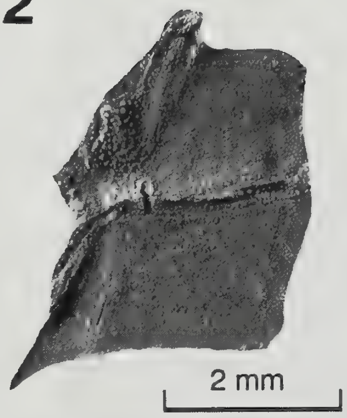

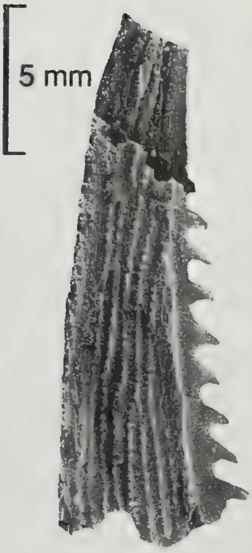

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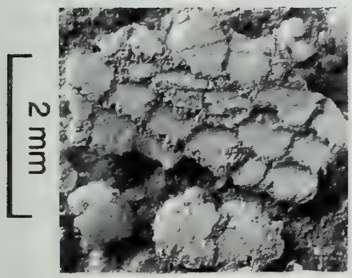
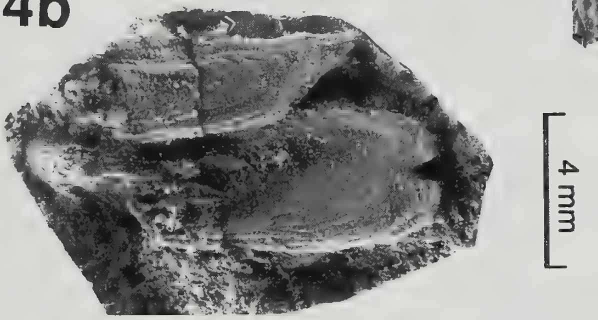
24a



24b



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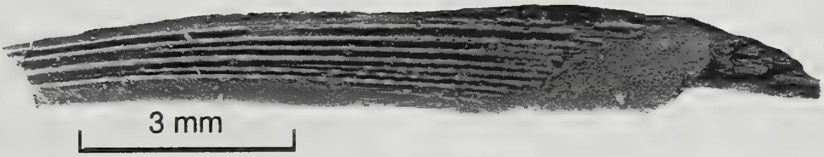

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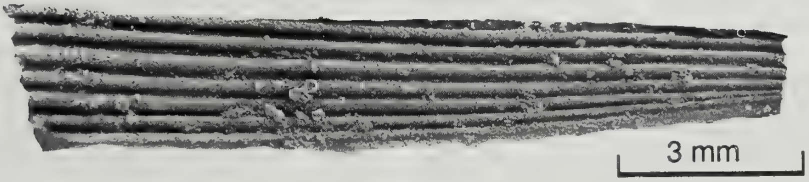

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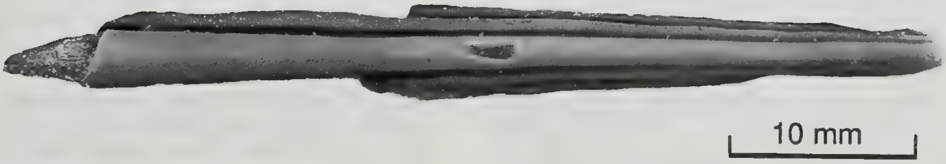

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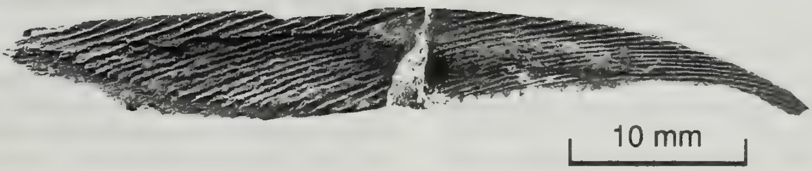

spine. The spine is straight with strongly defined ridges running parallel to the axis of the spine. The ridges are of varying thicknesses, and are arranged in an irregular manner. Sometimes adjacent ridges merge to form a single ridge distally. Some of the ridges show a faint overlapping, ribbed ornament, similar to that of many climatiid spines, and these ornament nodes are aligned slightly obliquely to the ridges and to the spine. P62857 is 73 mm in length, and is preserved as an impression with some of the bony tissue still remaining. The spine is slender and is almost straight, with a very slight curvature. About 8 or 9 strongly defined ridges run parallel to the axis of the spine, and are ornamented with faint ribs which run obliquely outwards from the proximal end of the spine and towards the posterior margin of the spine. These features are most similar to the anterior dorsal spine of *Parexus*. However, unlike *Parexus* the posterior margin of spine number P62857 is strongly ribbed with oblique, closely spaced ribs which are orientated posterodistally. No posterior denticles are evident along the posterior margin of spine number P62857 as they are in *Parexus*. Thus while specimen number P62857 has similarities to *Parexus* and may be closely related,it does not seem to be a species of this genus.

Order **ISCHNACANTHIDA**
Family **ISCHNACANTHIDAE** Woodward 1891

Genus ***URANIACANTHUS*** Miles 1973 [spines]

Uraniacanthus spinosus Miles 1973 Figs 26, 27

MATERIAL. Two fin spines, P62860 and P62861, each preserved as impressions, and each incomplete. Both are from sample 9, Jauf Formation.

REMARKS. Latex rubber casts were prepared from the natural moulds. The remaining portion of P62860 is 41 mm in length, and for P62861 is 26 mm in length. The spines differ, and resemble different fin spines of this taxon.

Specimen P62860 is slender, elongate and straight with smooth, unornamented longitudinal ridges. A relatively wide, convex ridge forms the anterior margin of the spine, and on each side are deep grooves and two or three well defined and quite broad ridges. The ridges or grooves are parallel to the length of the spine and do not merge along the portion of the spine which is preserved. This spine has several similarities to *Devononchus* and to the posterior dorsal and pelvic spines of *Uraniacanthus spinosus*. In all of these the spines are slender, straight or nearly so, and have a wide convex longitudinal ridge along the anterior margin. On each side there are several strongly defined ridges and grooves, which run parallel to the axis of the spine, and which are smooth and unornamented. The spine from Saudi Arabia (P62860) has three ridges on each side of the anterior ridge. Five ridges are present on each side of *Devononchus*, and on the posterior dorsal and pelvic spines of *U. spinosus* two ridges are present. *Devononchus* is considerably larger than specimen P62860, the spines of *U. spinosus* are more comparable in size. The insertion area of *Devononchus* is relatively significantly longer than that of specimen P62860. Thus, specimen P62860 is more closely comparable to the posterior dorsal and pelvic fin spines of *U. spinosus* from the Lower Devonian (Upper Gedinnian), Dittonian, of Herefordshire (Miles 1973).

Specimen P62861 is very gently curved, and has seven strongly pronounced, smooth, unornamented, narrow ridges, parallel to each other and to the axis of the spine. The ridges remain separate and do not merge along the portion of spine preserved. An impression of a small portion of the anterior margin of specimen P62861 is preserved, and its shape suggests that the spine is somewhat flattened in section, laterally or dorsoventrally. Specimen P62861 is very similar to the pectoral or anterior dorsal spine of *U. spinosus*.

Gen. et sp. indet. [tooth whorls] Figs 8, 9

MATERIAL. Specimens P62866, P62867 from sample 3 represent symphysial tooth whorls. P62867 is the best preserved (Fig. 8) and shows five teeth, the longest of which is 2·8 mm long. Each tooth is monocuspid, and is sharply angled so that the point is directed away from the adjacent tooth. The teeth each form a sharp point at the tip and the upper part of the tooth has a slight lateral ridge but is otherwise smooth (cf. the striated teeth of *Onychodus*). The tooth whorl seems to be a median structure and is typical of tooth whorls described for members of the Ischnacanthidae. The Ischnacanthidae range from Upper Silurian (Ludlovian) to Upper Carboniferous (Westphalian B) from North America, Spitsbergen, Europe, Siberia and Iran (see Denison, 1979).

Specimen P62853 (Fig. 9), sample 9, contains a small fragment of a symphysial tooth whorl. The hollow base is swollen and there are the bases of at least six teeth preserved. It looks very similar to small tooth whorls found in the Downtonian of the Old Red Sandstone of the Anglo-Welsh basin and described as *Onychodus anglicus* Woodward 1888. These whorls are almost certainly those of climatiid acanthodians probably more correctly referred to the genus *Gomphonchus*.

Family **GYRACANTHIDAE** Woodward 1906 [spines]

cf. ***Gyracanthus incurvus*** Traquair 1890 Fig. 28

MATERIAL. Seven specimens, all from the Wajid Sandstone, represent acanthodian spines which have a characteristic ornament comparable to that in *Gyracanthus incurvus*.

REMARKS. The largest and best preserved of the spines (P62814a, b) is 52 mm long. P62816a, b is 16·5 mm long: P62811 and P62813a, b are an estimated 50 mm and 43 mm in length respectively, while the remaining three specimens P62812, P62810 and P62815a, b are fragments of spines only. The three more complete specimens show this spine to have a broad, shallow base of insertion as in spines of climatiids in general. They are gently curved, this curvature becoming more marked at the distal end, and the spine is ornamented with prominent ridges. The ridges on either side run obliquely across the spine and intersect one another in a chevron pattern along the leading edge. There are 20–22 ridges at the base of the spine, which is 17 mm wide in P62814a, b. Although the ridges appear smooth distally they are faintly nodose at their bases. The largest spine carries about 25 recurved denticles along the posterior edge.

These spines are comparable with those of *Vernicomacanthus* and *Gyracanthus* in that the ornament consists of ridges which intersect the leading edge and are faintly nodose, particularly at the base. The two recognized species of *Vernicomacanthus* are smaller than the Saudi specimens and the ridges, of which there are far fewer, are more strongly nodose. The Saudi spines are more comparable in size with *Gyracanthus incurvus* and there are about the same number of ridges which tend to be smooth except at the base. *G. incurvus* also has a series of posterior denticles, although there appear to be far fewer in the Saudi specimens. *G. incurvus* comes from the Lower/Middle Devonian of Campbellton, New Brunswick (Woodward 1892). Blieck *et al.* (1980: fig. 7) described spines from the Eifelian of Iran which look very similar to those described here, except that there do not seem to be any posterior denticles. This may be a preservational artefact.

Other acanthodians [spines]

Nodonchus cf. ***bambusifer*** White 1961 Figs 31, 32

MATERIAL. Three spines; P62871, P62859 from samples 8, 9 in the Jauf Formation, P62868 from the Wajid Sandstone.

REMARKS. The three spines are dissimilar in shape, but have a similar ornament. The spines have several longitudinal ridges. Their ornament of overlapping ribs and the shallow broad base of insertion of the spines suggest that they belong to the Climatiidae. Together they represent spines from different parts of the body. P62871 is a small fragment from the base of a flattened spine and shows about fifteen ornamented ridges, some of which merge. P62859 is an almost complete spine 41 mm in length, slightly curved, gently convex and tapering rapidly distally. A large part of the insertion area is present, and is set at an angle of 35° to the axis of the spine. P62868 is 21mm in length, stout and rapidly tapering, and may be a spine from an intermediate series. P62859 and P62868 both show a broad base of insertion. The ornament ridges remain separate from one another and taper to match the overall tapering of the spine. The ornament is of truncated nodes developed symmetrically along the axis of each ridge (cf. the asymmetrical nodes of *Climatius latispinus*) although each truncation is set at a shallow angle. The pattern and spacing of ornament is similar to that of *N. bambusifer* White 1961 (Lower Siegenian, Shropshire, England), the difference being that the spines from Saudi Arabia are more flattened.

Subclass **CHONDRICHTHYES**
Infraclass **ELASMOBRANCHII**

Genus ***ANTARCTILAMNA*** Young 1982

Antarctilamna sp. Figs 29, 30

Three specimens (P62817a, b, P62818 and P62819a, b) from the Wajid Sandstone consist of groups of scattered, small compound scales preserved as impressions. No histological details are preserved but sufficient surface topology remains to suggest that they belong to *Antarctilamna* and that these scales may be associated with *Antarctilamna*-like spines also found in the Wajid Sandstone. Each scale is ovoid to circular, about 2 mm in the greatest diameter, and since they are all about the same size on each of the scatters they probably each represent single portions of the squamation. The crown of each scale is rather flat and the base is much smaller, located at the anterior end and is connected to the crown through a neck. This is typical of some Silurian and Devonian elasmobranch scales (*Cladolepis* Wells 1944, Gross 1973; *Maplemillia* Gross 1973; *Elegestolepis* Karatajute Talimaa 1973; *Ellesmereia* Vieth 1980; *Antarctilamna* Young 1982). Other elasmobranch scales show a base and crown of roughly equal size. The Wajid scales, like those of *Cladolepis* and *Antarctilamna* show a surface ornament of long ridges which tend to follow the margin of the crown, together with an area anteriorly which is covered with small, partially recumbent, grooved spines. These scales are uniquely like *Antarctilamna* in having an open cup-shaped base.

Antarctilamna prisca Young is known from late Givetian/early Frasnian of south Victoria Land and New South Wales. Gagnier *et al.* (1988) described a second species, *A. seriponensis* from the Emsian of Bolivia. *Antarctilamna* probably also occurs in the Eifelian of Iran (see Young 1989: 50) because the spine illustrated by Blieck *et al.* (1980: pl. 1, fig. 20) and described as having *Ctenacanthus* type ornament is indistinguishable from *Antarctilamna*.

Four specimens of fin spines may belong to *Antarctilamna*. P62820, P62822, P62823 and P62821 are all short, stout spines. P62821 (Fig. 29) is by far the best preserved, measuring about 25 mm long and being 15 mm broad at the base. These proportions are similar to the larger spines of *Antarctilamna* figured by Young (1982: pl. 87). The spines are nearly straight with a narrow zone of insertion. They are marked with prominent costae which are composed of cone in cone ornament. In this they resemble ctenacanth spines but, as Young (1982) pointed out, this type of ornament may have been the primitive elasmobranch type found in both ctenacanths and xenacanths. In P62821 there are about eight costae on either side of the midline. P62822 and P62823 represent parts of larger spines in which there are approximately 13 costae on either side, a number more like that found in *Antarctilamna prisca* Young. The number of costae may simply reflect size.

Family **PHOEBODONTIDAE** Williams 1979

Genus ***PHOEBODUS*** St John & Worthen 1875

Phoebodus sp. Fig. 7

A single tooth (P62874) in sample 22 from the Jauf Formation represents a diplodont tooth and although broken, enough remains to allow determination as a tooth of *Phoebodus*. The base is tumid, pierced by four relatively large nutritive foramina (cf. *Antarctilamna* where the base is pierced by many formina, Young 1982: fig. 3). The crown has two lateral and slightly divergent cusps with three inner cusps. Unlike named species the inner cusps tend to be rather small. An isolated cusp on the same specimen shows faint striations and such were mentioned for the type species *P. sophiae* by St John & Worthen (1875). *Phoebodus* species are known from the Middle Devonian to Upper Carboniferous of North America, although it is highly likely that some of the younger forms should more properly be referred to other genera.

Form genus '***CLADODUS***' Agassiz 1843

There are many teeth present in sample 9 (preserved on specimens P62855 and P62856) which can only be referred to the form genus *Cladodus*. These are Palaeozoic shark teeth

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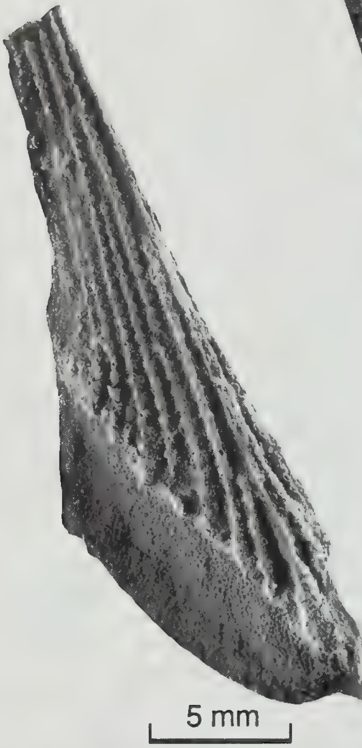

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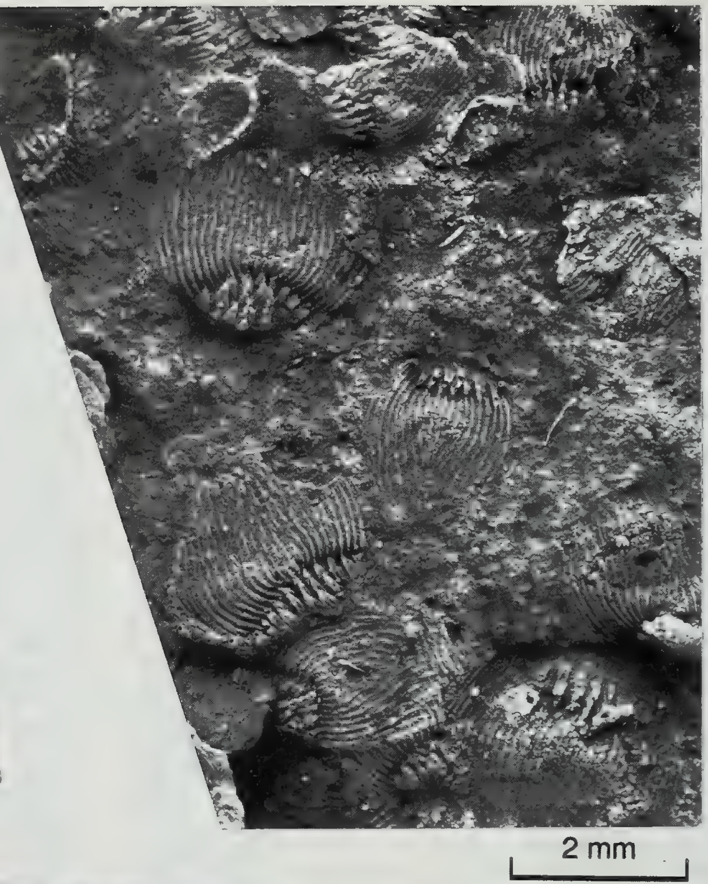

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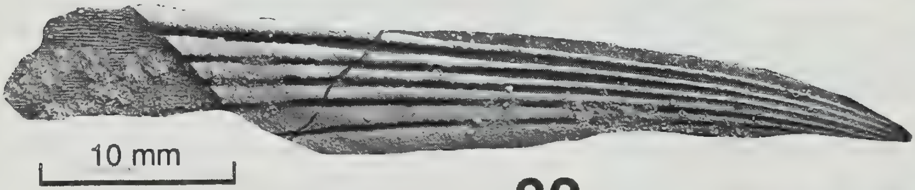

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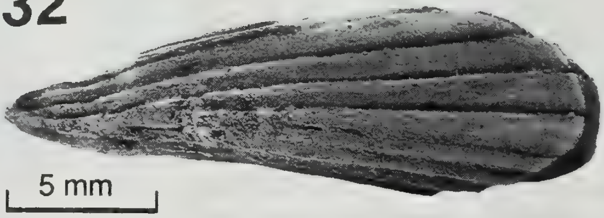

Figs 29–30 *Antarctilamna* sp. 29, spine P62821 (cast). 30, group of scales P62819a (cast).
Figs 31–32 *Nodonchus* cf. *bambusifer* White. 31, median spine P62859 (cast). 32, intermediate spine P62868 (cast).

with a long central cusp and two or three much smaller lateral cusps. They are known from the Lower Devonian onwards. In the Saudi Arabian sample these teeth are rolled and worn such that usually only the central cusp remains on the swollen root. The central cusp may reach 8 mm in length. The lingual surface of the cusp is striated at the base.

ACTINOPTERYGII

Rare actinopterygian scales have been found in samples 15 and 26, Jauf Formation. They are rectangular in outline and show a convex base. The outer surface is marked by a prominent diagonal ridge passing anterodorsally–posteroventrally. There are a few minor ridges which follow the principal ridge.

DISCUSSION

The discussion which follows deals briefly with comparisons between the Saudi Arabian fish fauna described here and some other fish faunas of the Devonian. Despite being

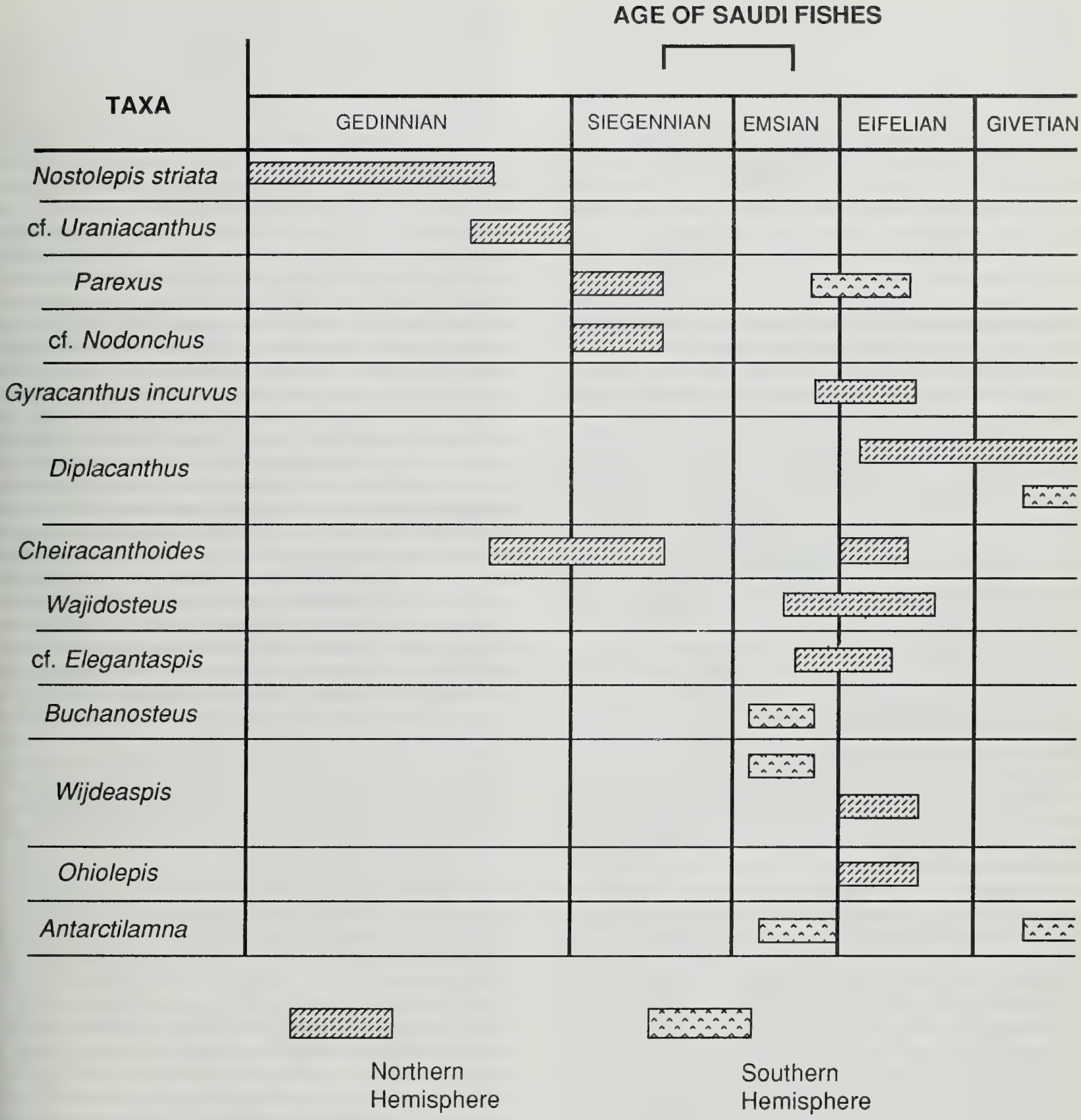

Fig. 33 Chart comparing the stratigraphical distribution of some of the taxa found in the Saudi Arabian fauna with comparable taxa elsewhere in the world.

represented by fragmentary material, the present fauna adds to our knowledge of Devonian fishes from the Middle East. Its significance may only be assessed within the context of biostratigraphical and biogeographic comparisons. Boucot *et al.* (1989) estimated the age of the Jauf Formation invertebrate fauna as Pragian–Early Emsian and the fishes do not contradict this determination, which is therefore accepted here.

Figure 33 shows the stratigraphic distribution of the Saudi Arabian fish taxa, or near relatives, plotted against those same taxa occurring in other parts of the world. Because Saudi Arabia lay near the equator in Lower Devonian times (Scotese & McKerrow 1990), it is pertinent to show comparisons with reference to both northern and southern hemisphere fish occurrences. Fish faunas of exactly the same age are very rare, although they may be represented in Spitzbergen (Wood Bay Series) and perhaps Canada (Battery Point Formation and Atholville Beds). For those taxa found both in Saudi Arabia and in northern hemisphere faunas, then, the match is either with contemporaneous taxa (cf. *Elegantaspis*, *Gyracanthus incurvus*) or with taxa which are older than in Saudi Arabia (*Uraniacanthus*, *Parexus*, *Nodonchus*). For those shared between Saudi Arabia and the southern hemisphere the match is either with contemporaneous taxa (*Buchanosteus*, *Wijdeaspis*) or younger (diplacanthid, *Antarctilamna*). This raises an interesting question, since Saudi Arabia was firmly part of Gondwana in Lower Devonian times and was supposedly separated from northern landmasses such as Laurentia, Baltica, and Angaraland by a Rheic ocean (Scotese & McKerrow 1990). It might therefore be expected that taxa which are represented in deposits which are older elsewhere would have southern hemisphere affinities. In fact it is quite the reverse (also see below).

Leaving this point aside temporarily, the total aspect of the Saudi Arabian fish fauna is recognized as 'Gondwanan' as characterized by Young (1987). For instance, the Saudi Arabian fauna consists only of acanthodians, placoderms and sharks (with a few actinopterygian scales). There are no heterostracans, osteostracans or galeaspids. This negative evidence, of course, might be explained by the fact that Saudi Arabia lies outside any of the Provinces containing these taxa (Young 1981). With a few exceptions, the absence of these taxa in Lower Devonian deposits is typical of Gondwanan faunas. The absence of thelodonts cannot be explained on straight geographic grounds because Saudi Arabia should lie well within the *Turinia* province (Turner & Tarling 1982). The absence of thelodonts may be a facies problem. There are also no actinolepid placoderms. Their rarity is an acknowledged feature of Lower Devonian Gondwanan faunas (Young 1987). On the positive side, the presence of *Antarctilamna* ties it to Gondwana since this is found in younger deposits of Antarctica and Australia, but it is also found in roughly contemporaneous deposits of Bolivia, South America (indet. chondrichthyan, Gagnier *et al.* 1989*b*: *Antarctilamna seriponensis* Gagnier *et al.* 1988). As far as we know, *Antarctilamna* is exclusively southern hemisphere. The evidence from structural geology and palaeomagnetism suggests that Arabia was part of northern Gondwana, probably lying 15°–30° south of the Lower Devonian equator (Scotese & McKerrow 1990). But does the fauna agree entirely with our concepts of Gondwanan fish faunas and how does it relate to other fish faunas? Figure 33 shows that there are more associations with taxa in the northern hemisphere. This may reflect true historical pattern or bias in collecting and description. The acanthodians, in particular, appear to have closer affinities with those in the northern hemisphere. Most of these are climatiids which are generally rare in the southern hemisphere. Exceptions may be some climatiid remains from the Lower Devonian (?Gedinnian) described from Brazil (Janvier & Melo 1988). *Nostolepis* scales are found in S. China (Gagnier *et al.* 1989*a*). So it is possible that climatiids and perhaps ischnacanthids were worldwide at the beginning of the Devonian. Amongst the climatiids there is a particular similarity with *Gyracanthus incurvus* of eastern Canada. On the other hand one of the diplacanthid acanthodians is closely similar to the un-named diplacanthid from Antarctica. Amongst the placoderms, then, the similarity of *Wajidosteus* and *Elegantaspis* with phlyctaeniids from eastern Canada and Spitzbergen is important. But the other placoderms tell a different story. *Buchanosteus* is an Australian form, although we know of close relatives in S. China and in Iran (Goujet & Janvier 1989), perhaps also in Kazahkstan (Lelièvre 1989). The petalichthyid *Wijdeaspis* is known from Australia, but is also found in Spitzbergen and, in slightly younger rocks, in Siberia. Petalichthyids, like climatiids, may well have been world wide in the early Devonian. Finally, *Antarctilamna* is elsewhere found in the southern hemisphere, although it needs pointing out that the Saudi collection does contain scales resembling *Ohiolepis* which are elsewhere found in the northern hemisphere, as are the teeth *Phoebodus* and *Cladodus*.

This rather intermediate position of the Saudi Arabian fauna, with elements traditionally regarded as both of northern and of southern hemisphere origin, requires some explanation. The first question we may ask is: is this fauna unique? If so it may just be a quirk of sampling. Faunas which are geographically and stratigraphically nearby include those from localities in North Africa and Iran. The area immediately adjacent to Saudi Arabia is Iran even though most of Iran was located on a different plate closely adjacent to the Arabian shield (Scotese & McKerrow 1990: fig. 14). The northern Iranian fish locality of Khush Yeilagh is usually regarded as slightly younger than the Saudi locality, being early Eifelian in age, although some work by Hamdi & Janvier (1981) on the condonts of the beds overlying the fish-bearing parts of the Khush Yeilagh Formation suggests an Emsian age. The Iranian fauna has been described by Blieck *et al.* (1980). It is far more diverse than that of Saudi Arabia but there are some common elements. Buchanosteids are present in both, as are elasmobranch spines resembling *Antarctilamna* (Blieck *et al.* 1980: pl. 1, fig. 20) and there is a very similar *Gyracanthus* spine (1980: fig. 7C, D). The Iranian fauna also includes small phlyctaeniids, although none appear conspecific with those from Saudi. The Iranian fauna is usually compared with those of Gondwana and China. *Antarctilamna* is certainly Gondwanan. Buchanosteids are shared with both eastern Australia and China which may be considered closely tied to Gondwana. But it is worth noting that buchanosteids may also be present in Kazakhstan (Lelièvre 1989), a truly northern locality. Janvier (*in* Blieck *et al.* 1980) identified some trunk plates of an antiarch from Iran as being closely similar to a form from the Middle Devonian of south China (*Hyrcanaspis* Janvier & P'an 1982). Many other elements of the Iranian fauna are not obviously Gondwanan and have affinities elsewhere. Goujet (*in* Blieck *et al.* 1980) thought that the small phlyctaeniids were like those of the Emsian–Eifelian of Quebec. Mark-Kurik thought that the holonematids were like those of the Baltic. Goujet thought that the coccosteids were similar to those of Scotland and that the groenlandaspids were more like those of Germany than of Australia. Janvier thought that the acanthodians and the sarcopterygians were similar to those of Germany as well as the Baltic and North America (all *in* Blieck *et al.* 1980). There is therefore a similar pattern to the fauna from Saudi Arabia. Both have a Gondwanan (and south China) element but it is nevertheless overshadowed by animals more similar to those occuring in northern areas.

From Morocco, Lelièvre (1984, 1988) has described Emsian arthrodires *Atlantidosteus* and *Antinosteus* which can be demonstrated to have sister taxa in the Emsian of eastern Australia. But there is nothing in common between Saudi Arabia and Morocco. Other localities which may be of significance are found in northern Spain and Rhenish Bohemia, associated with remnants of plates dubbed as Armorica. Armorica has always been problematical, even to details of recognizing what constitutes Armorica (see Young 1987:286), but most workers recognize that Armorica began its history as part of Gondwana (Cocks & Fortey 1982). There are very few taxa shared between the Lower Devonian of Spain and Saudi Arabia or Iran. The Spanish localities have been described by Mader (1986) and most of the taxa there have northern affinities, including the presence of heterostracans. It has to be said that the Spanish localities are predominantly Gedinnian in age, much earlier than the Saudi Arabian or Iranian faunas. The other localities, of which there are a great number, are found in the Pragian and Emsian Hunsrückschiefer. There is a large fauna here (Gross 1951) and it contains typically northern fishes such as cephalaspids and heterostracans, as well as placoderms such as *Gemuendina* and *Lunaspis* which are closely related to forms in South America and eastern Australia respectively, with *Lunaspis* being additionally found in China (Liu 1981). It also contains *Speonosydrion*, a dipnoan originally described from the Emsian of eastern Australia. The fish faunas of Rhenish Bohemian localities show some similarity with the fauna from Saudi Arabia and Iran. There are similar placoderm scales. The tiarapsid-like groenlandaspids and some acanthodian spines of Iran suggest Rhenish Bohemian affinity (Blieck *et al.* 1980). With the invertebrate evidence from Saudi Arabia (Boucot *et al.* 1989), such as one trilobite species which is only found elsewhere in Rhenish Bohemia and two brachiopod species known from northern Spain, this may be confirmation that the Lower Devonian Saudi Arabian fauna belongs with that of northern Iran and with the Rhenish Bohemian faunal province. How the Rhenish Bohemian endemism was established is more problematical. To consider it as Gondwanan may be over-simplified (see also Young 1990:247) because this is a huge area spread over a large part of the southern hemisphere. The faunas of eastern Gondwana (eastern Australia and part of Antarctica) contain fishes (e.g. wuttagoonaspids) sufficiently distinct to justify characterizing an East Gondwana province (Young 1981) which, in turn, may have closer connections with south China than anywhere else. On the other side of Gondwana, the newly described Devonian fish faunas of Bolivia (Gagnier *et al.* 1988) and Brazil (Janvier & Melo 1988) show similarity, albeit not a unique similarity, with North America and the Rhenish Bohemian province (rhenanids, *Machaeracanthus*). With such limited amounts of information detailed conclusions about more distant associations cannot be justified. Without cladograms and theories of sister-group relationships there is little chance of being able to tie two areas together to the exclusion of others.

With the present state of knowledge we can say that the Saudi Arabian fauna probably belonged within the Rhenish Bohemian area of endemism in the late Pragian/early Emsian and no doubt this area of endemism was independent from the Euramerican basin as described by Blieck (1982). But there are some elements of the Saudi Arabian fauna chiefly the phlyctaeniids, petalichthyids and some of the climatiids which suggest an earlier connection with more northern areas, perhaps before a vicariance event created the Euramerican and Rhenish Bohemian faunal realms.

We conclude that the Lower Devonian fish fauna from Saudi Arabia discussed here belongs with that of the Rhenish–Bohemian Province, but that there are affinities with older faunas in the northern hemisphere and younger faunas in the southern hemisphere.

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APPENDIX

List of sample numbers with brief lithological description and fauna. Samples presented in stratigraphical order (see Fig. 2). Sample numbers are the original numbers given in the field. Geographical localities are indicated in Fig. 1.

Sample 3 29°49·7′N 39°50·4′E, Jal al Gharb, Jauf Formation, Shai'ba Member, about 30 m below top. Light grey-green, grey, and maroon, fissile, partly silty shale with a few grey-tan, fine crystalline dolomite streaks, and common small phosphate grains and very small rolled bone fragments. Petalichthyid P62862, P62863a, b; *Wajidosteus* P62865; ischnacanthid tooth whorls P62866, P62867; *Nostolepis striata* scales. Probable depositional environment: quiet brackish water in mud lagoons.

Sample 9 29°27′N 38°27′E, Ja'alat as Sawada, Jauf Formation, Sha'iba Member, about 6 m above base. Hard, red, fine-grained, black-weathering ferruginous sandstone. *Gomphonchus* symphysial tooth whorl P62853; *Cladodus* P62854–6; indet. climatiid spines; *Nodonchus bambusifer* P62859; *Uraniacanthus spinosus* P62860, P62861; climatiid indet. spine P62857, P62858; *Nostolepis striata* scales. Probable depositional environment: flood plain or fluvial channel outwash, deposited in minor sea level lowering event during Shai'ba times. Red colour suggests penecontemporaneous oxidation.

Sample 8 29°27′N 38°27′E, Ja'alat as Sawada, Jauf Formation, Sha'iba Member, about 32 m above base. Yellow to light red, very hard, fine grained sandstone with thin, silicified lenses just below top. Conchostracans; *Rhabdostichus* sp.; eurypterids cf. *Willwerathia* or *Rhenopterus*; a single lingulid; *Parexus* P62870; *Nodonchus bambusifer* spines P62868, P62871; *Wajidosteus* P62869. Probable depositional environment: presence of conchostracans lends support to a non-marine aspect (the one lingulid may be due to backwash or reworking from a near shore marine environment); the yellow and light red colours suggest penecontemporaneous oxidation due to subaerial exposure.

Sample 11 29°28′N 39°34′E, near Barqa As-Sha'ira, approx. 47 km southwest of Al Jawf, about middle of Subbat Member. Yellow, partly porous and hard, calcarenitic, very fossiliferous limestone/dolomite stringer. Apparently not present in type section area. Petalichthyids P62949 and P62950; corals, bryozoa, brachiopods and bivalves. Probable depositional environment: shallow water marine environment.

Sample 7 29°55′N 39°48·5′E, Ajrabah, Jauf Formation, Subbat Member, about 47 m below top. Grey and grey-tan, argillaceous and calcareous siltstone and grey silty shale. Lingulids very common; eurypterid impressions; *Onchus* spines P62873 and P62872. Probable depositional environment: quiet brackish water in mud lagoons.

Sample 24 29°55′N 39°48·5′E, Ajrabah, Jauf Formation, Subbat Member about 32 m below top. Light golden yellow, soft fine grained sandstone stringers in shale. *Jaufolepis striata* gen. et sp. nov. (P62957a, b). Probable depositional environment: fluvial outwash during minor sea lowering event.

Sample 25 29°51′N 39°52·7′E, near Al Jawf Gardens, Hammamiyat Member, 2–3 m above top of first Hammamiyat limestone. A thin grey-tan, hard, dense, limestone/dolomite stringer. Many fish fragments representing unidentifiable phylctaeniid arthrodires; *Buchanosteus*; brachiopods, corals, bivalves, bryozoa and ostracods. Probable depositional environment: shallow water marine environment.

Sample 26 29°50·8′N 39°52·6′E, Subbat el Wadi, Jauf Formation, base of Transition Zone Member. Yellow soft, friable, medium grained sandstone, with rip up clasts of underlying grey clay. *Nostolepis striata* scales (P62952), actinopterygian scales, diplacanthid scales (P62951). Probable depositional environment: fluvial channel or channel outwash.

Sample 15 30°01·7′N 39°58·2′E, Tell al Murair, Jauf Formation, top of Transition Zone Member. Soft sandstone, fine grained, micaceous, with red siltstone streaks and rip up clasts of underlying channeled grey clay. *Nostolepis striata* scales (P62954), *Cheiracanthoides* scales (P62953), actinopterygian scales, diplacanthid scales, actinolepid trunk plates. Probable depositional environment: shallow, possibly braided, fluvial channel.

Sample 17 30°4′N 40°5′E, Qiyal Sagiyr, Jubah Sandstone, about 40 m above top of Jauf Formation. Red siltstone and fine grained, soft and friable, white speckled sandstone. Many broken and rolled fish scales and plates, all difficult to identify. Some plates have ornament reminiscent of *Buchanosteus* (approximately regular tubercles, stellate at the base) but this type of ornament is by no means restricted to this genus. Scales include those of placoderms (P62958–60) and those of *Nostolepis striata* (P62956). Probable depositional environment: high energy fluvial channel outwash or flood plain; red colour suggests penecontemporaneous oxidation due to subaerial exposure.

Sample 22 30°13·6′N 40°09·2′E, Adhiriyah, Jubah Sandstone, about 110 m above top of Jauf Formation. Very hard, tan, fine grained sandstone capping yellow shale, with small pockets of softer, red, fine grained sandstone with phosphate pellets and rolled fish remains. One lingulid brachiopod; broken acanthodian spines; diplacanthid scales, a scale of *Cheiracanthoides* sp. (P62955); *Phoebodus* sp. (P62874). Probable depositional environment: high energy fluvial channel outwash or a flood plain (the one lingulid may be due to backwash from a nearby shallow-water marine shore environment).

Wajid Sandstone 17°36′N 44°5·5′E. Fine, very silty and well indurated, varicolored micaceous claystone. *Gyracanthus incurvus* (P62810, P62811, P62812, P62813a, b, P62814a, b, P62815a, b, P62816a, b); *Antarctilamna* (P62817a, b, P62818, P62819a, b, P62820, P62822, P62823, P62821, P62824, P62825); *Wajidosteus minutus* (P62826, P62827, P62828, P62829, P62830, P62831, P62832, P62833a, b, P62834a, b, P62835a, b, P62836a, b); cf. *Elegantaspis* (P62837); petalichthyid (P62838); phlyctaeniids (P62839, P62840, P62841, P62842, P62843, P62844, P62845a, b, P62846a, b, P62847a, P62848); actinolepid (P62849a, b); *Nodonchus bambusifer* spine (P62868). Probable depositional environment: very quiet water in restricted basin, possibly a cut-off lagoon.

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W. K. Parker's collection of foraminifera in the British Museum (Natural History)

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SYNOPSIS. William Kitchen Parker (1823–1890) was associated with H.B. Brady, W.B. Carpenter, T.R. Jones and W.C. Williamson, and amassed in his lifetime a considerable collection of Recent and fossil foraminifera. It was purchased by the British Museum (Natural History) in 1892 from his executors, there to be identified and catalogued by Professor Thomas Rupert Jones. This article provides information on the Catalogues and the new species erected by Parker and his associates. Lectotypes have here been selected and illustrated for the following taxa: *Anomalina coronata*, *Articulina multilocularis*, *Hauerina plicata*, *Hippocrepina indivisa*, *Lagena crenata*, *L. distoma*, *L. sulcata* var. *distomapolita*, *L. sulcata* var. *marginata* subvar. *squamosomarginata*, *L. sulcata* var. *tetragona*, *L. sulcata* var. *tubiferosquamosa*, *Lituola cassis*, *L. findens*, *L. nautiloidea* var. *soldanii*, *Polymorphina elegantissima*, *P. frondiformis*, *P. regina*, *P. variata*, *Polystomella arctica*, *Pulvinulina concentrica*, *Rotalia beccarii* var. *annectens*, *R. beccarii* var. *dentata*, *R. schroeteriana* and *Uvigerina* (*Sagrina*) *dimorpha*. Several 'lectotypes' chosen elsewhere by other authors, for *Discorbina rimosa*, *D. turbo* var. *polystomelloides*, *Lagena sulcata* var. *striatopunctata* and *Trochammina squamata* var. *gordialis*, shown to be invalid because they were not syntypes, are all regarded as neotypes. A brief biography of Parker is given.

THE COLLECTION

William Kitchen Parker's sudden death on July 3rd, 1890 set in train a series of events which resulted in his collection of foraminifera being deposited in the British Museum (Natural History), London. His executors attempted to realize as much money as possible from the estate, and his son W.N. Parker, on advice from Professor T.R. Jones, approached the Trustees of the British Museum (Natural History) offering the collection of foraminifera for sale. The Director, W.H. Flower, authorized the purchase, funded jointly by the Departments of Zoology and Geology (now Palaeontology), for £100. The collection came to the Museum in 1892 and was said to comprise about 2000 fossil and 1000 Recent slides, most containing many genera and species. The number of specimens this added to the collection is difficult to estimate, but was considerable. T.R. Jones, a long term friend and collaborator of Parker, was keeping a wary eye on the specimens, for he wrote to the Keeper of Zoology A.C.L.G. Günther that he would be ... 'glad to carry on the arrangement' (of the specimens). In June 1892 Jones met R. Kirkpatrick, a curator at the Museum, to discuss the collection. This led, on June 25th, to both Dr Günther and the Keeper of Geology Dr A.S. Woodward jointly requesting authority to employ Jones in 'naming, labelling and arranging the collection of Recent and fossil foraminifera purchased from the executors of the late Professor W.K. Parker'. The Director recommended and the Trustees approved, but stipulated that the payment for this work was not to exceed £80 (being divided equally between the two Departments) and every 100 slides curated would provide Jones with £1 17/6d (£1.88p). By the middle of 1894 Jones seems to have completed his work, for records of Geology Department payments cease on June 4th. The result of his labours is a well-arranged collection and a manuscript catalogue for both the Recent and Fossil parts of the collection. This collection and its catalogues are housed in the Micropalaeontology Section of the Department of Palaeontology, British Museum (Natural History), London.

THE CATALOGUES

There are two catalogues, herein referred to simply as the Catalogue, Fossil and Recent being specified when necessary. Inside the Recent volume there is an indication that it was not bound until 1937, possibly at the instigation of Edward Heron-Allen (Hodgkinson 1989); the Fossil volume may have been bound earlier. Both catalogues are bound in blue, titled along the spine in gold lettering, thus:

CATALOGUE OF FOSSIL FORAMINIFERA EC.
PARKER COLLECTION T. RUPERT JONES
INDEX TO BOXES I–XLV 1894

and

CATALOGUE OF PARKER COLLECTION
RUPERT JONES INDEX TO BOXES I–XXVII

The Introduction to the Catalogue, in what appears to be Jones' handwriting, is to be found in the front of the Recent manuscript and was probably written at the completion of the work. In it Jones makes the following comments.

1. 'Very often the figured specimens, though present in the collection cannot be easily defined'.
2. 'The collection was the basis of the "Notes on the Nomenclature of the Foraminifera", the papers of W.B. Carpenter in the *Philosophical Transactions of the Royal Society* of 1856, 1859 and 1860 and the *Introduction to the Study of the Foraminifera*, 1862'.
3. 'In naming the species, care has been taken to follow as closely as practicable the method of nomenclature used by W.K. Parker. Modern names for some genera, species and varieties are adopted when of real importance, having been founded on knowledge obtained since Prof. Parker left off working on his collection'. (I do not know when Parker 'ceased' to work on foraminifera in his lifetime, if he ever did, but his last taxonomic paper containing new species seems to have been published in 1872, when he was 49 years old, eighteen years before his death in 1890–R.L.H.).
4. 'The Published Lists and the Catalogue do not always correspond since some specimens may have been lost, others not noticed in the published lists either on account of their not being regarded as notable varieties or, not being contained in that part of the collection which was first studied when the lists were originally made. Some cannot be fully identified in the closed cells of the slide since only one side or face of the foraminifer is visible'.

Although Jones makes no comment in the Catalogue to the Recent foraminifera, in the Fossil Catalogue he does write: '*Note*–The names given in the Catalogue are to be taken, not any *other* names written on the slides themselves. . .' I assume the same applies equally to the names given in the Recent Catalogue. Who wrote the names on the slides still remains to be discovered.

Within the Recent Catalogue, the Introduction is followed by a *General Geographical List* and each locality is given a number in Roman numerals; for example:

North Atlantic Ocean
Britain
South Coast
Poole, Dorset VII

and the slides from those localities were also numbered (for example Poole, Dorset VII.1 and 2 etc.). Each group was then placed in boxes specially supplied for the purpose (Pl. 6, fig. 5, p. 73).

In 1937, Edward Heron-Allen, who as an unpaid curator was looking after the collection of foraminifera at the Museum, made a note in the Catalogue (see Pl. 4, fig. 2) that he had removed the slides from the boxes and arranged them by their numbers in 58 drawers so that they could be more easily examined. The only numbers which now need to be known are those written by Jones in pencil on the reverse of the slide and the individual Museum register number. Heron-Allen preserved the labels from the boxes by gluing them on to sheets of paper and filing them in a loose leaf ring binder labelled on the spine 'ORIGINAL LABELS from Boxes and Special slides'. Additional labels concerned with the H.M.S. Firebrand material are kept in the back of the Catalogue.

Following the *General Geographical List* is the *List of the Recent Foraminifera in the Parker Collection*, which tells the species content of each slide from a major and a sub-headed geographical locality, for example:

'**A. BRITISH** (North Atlantic Ocean) I. Southend on the Thames [6 slides, 4 good], see column 5 in Table VII

p. 422 ec Philos. Trans 1865 slide no. 1. . . no. 2. . . etc.'. (For actual examples of this see Pl. 4, figs 3, 4).

The Recent slides were catalogued (see below) between 1960–70 by Mr I.D.J. Burdett, a Scientific Assistant in the Department of Zoology.

The date of binding of the Fossil Catalogue is not known, but the date of its compilation is given on the spine as 1894. The Introduction is not in Jones' handwriting and differs slightly from that at the beginning of the Recent Catalogue in that it mentions publications in the *Quarterly Journal of the Geological Society* and *The Geological Magazine* and states that 'A Geological and Geographical order has been followed as nearly as circumstances permit'. 'The order of the species in the several lists is approximately in accordance with the zoological arrangement adopted in H.B. Brady's "Challenger Report", 1873–1876', published in 1884.

Between 1960 and 1970 these Fossil slides were taken from their boxes and placed in drawers and the complete collection was catalogued (see below) by Miss H. Patterson, an Assistant Scientific Officer in the Zoology Department, with some assistance from myself, then an Assistant Experimental Officer. Unfortunately, because the Museum's micropalaeontological collection is arranged stratigraphically, by collectors, the Fossil Collection could not be kept together, and it is thus more difficult to retrieve than the Recent Collection. The boxes have been kept, however, and all the labels are still in place (see the example on Pl. 6, fig. 5).

The information on the entire collection is filed in the retrieval system (indices to genera and species etc.) of the then Protozoa Section, now Micropalaeontology Section, Department of Palaeontology, B.M.(N.H.).

T.R. JONES' APPROACH TO IDENTIFICATIONS

In the main, H.B. Brady's work on the Challenger Foraminifera provided the basic framework on which Jones, in his Catalogue, based his revision of Parker's generic and specific names. Parker & Jones (1865: 335) adhered 'as strictly as possible to the plan of study laid down by Williamson 1858, and Carpenter 1862' and in their own papers of 1859–1863 (The Nomenclature of the Foraminifera) and they identified on the 'near approach to identity' method. This probably encouraged their frequent descriptions of new species, subspecies, varieties and subvarieties which seem to cause so much confusion to present day taxonomists. It is also possible that Jones, 20 years later when he came to prepare the Catalogue, was rather rushed and was unable to spend time identifying new, unfigured, varieties, which in his opinion and hindsight he might have considered junior synonyms of better known species. This is especially noticeable in the section dealing with the *Orbitolina concava* group. Sometimes he failed to notice syntypes on slides and thus they were not recorded in the Catalogue. It has been my policy to carefully examine these slides for missing types, often with success.

PROVENANCE OF MATERIAL

To those who are interested in the provenance of material, the Catalogues provide a valuable source and reference to the cruises of the oceanographic vessels, which were well known to the savants of Parker's time, but less so today. For the remaining samples, Jones sometimes gives the names of individual donors. Below, in alphabetical order, is a list of contributors.

Recent: H.M.S. Cyclops (Lieut. J. Dayman); H.M.S. Cyclops (Capt. W.J.S. Pullen); H.M.S. Firebrand (Com. J. Dayman); H.M.S. Fly (Capt. F.P. Blackwood; Jukes collection); W.E. Parry Expedition; H.M.S. Plumper (Capt. G.H. Richards); H.M.S. Porcupine 1862.

L. Barrett, W.B. Carpenter, H. Cristy, Mr Cummings, G.M. Dawson, G. Dines, W.J. Hamilton, A. Hilton, Sir Everard Home, W. King, R. McAndrew, Signor Meneghini, J. Millar, F.W. Millett, Colonel Pelly, Capt. T.A.B. Spratt, Marchese C. Strozzi, Dr Sutherland, G.C. Wallich, J. Wetherell, J. Wright, W.C. Williamson and S.P. Woodward.

For a discussion of the provenence of specimens from the Hunde Islands and their incorporation into the Parker Collection, see under *Textularia agglutinans* var. *biformis* (p. 63). Throughout the Catalogue Jones mis-spells Abrolhos as 'Abrohlos' (following mis-spelling in Brady, Parker & Jones 1888).

Fossil: D.J. Anstead, J.F. Blake, L. Barrett, J. Brown, Mr Burton, Cesare de Ancona, O. Fisher, Dr Haidinger, M. von Hantken, R. Harkness, W. Harris, Colonel Henekin, H.B. Holl, J.W. Hulke, Captain Hutton, M. Jokoyama, T.R. Jones, F. Karrer, A. Lennox, C. Lyell, Dr Meneghini, F.W. Millett, Sir Roderick Murchison, Mr Nugent, S.P. Pratt, Dr Prestwich, J. Purdue, A.W. Rowe, D. Sharpe, T.A.B. Spratt, J. Sinzow, H.C. Sorby, Dr Southby, J. Sowerby, R. Stachey, Marchese C. Strozzi, J. Szabo, Mr Thomas, Dr Thomson, M.E. de Verneuil, Mr White, S.V. Wood and J. Wright.

GENERAL REMARKS

During the 1939–1945 World War, the specimens were stored, but in 1953 when the Museum was almost fully recovered, A.R. Loeblich jr and H. Tappan examined the collection whilst preparing the *Treatise* (1964). Over a period of 35 days, they sifted through all the type slides, and finally selected lectotypes for 22 species.

A century has now elapsed since Parker died and T.R. Jones started his Catalogue. Many of the genera and species, both calcareous forms and those with agglutinated tests, are currently being restudied (Jones 1984, Brönnimann & Whittaker 1988, Gibson *et al.* 1991 and Kaminski *et al.*, in press) and it now seems opportune to examine the complete collection again and where possible update some information. I have tried, first, to find the syntypes, select lectotypes (with illustrations if necessary) of the remaining species and provide information on the type specimens; and secondly to list the collectors of Parker's material.

A third aim has been to prepare reference lists of the publications used by T.R. Jones to identify genera, species, varieties etc. As far as I am aware, there were never any lists accompanying the collection and the identifications were all undertaken for the Catalogue by Jones himself from these publications. Though not given here, these publication lists are available for private study at the Museum, in unedited form; the references given here (p. 75) are for the present text only.

H.B. BRADY'S USE OF MANUSCRIPT NAMES

Brady worked in close collaboration with Parker and Jones. Brady, whose manuscript on the Shetlands' Rhizopoda was read in February 1864, possibly attributed the names of three species (*Lagena distoma*, *Polystomella arctica* and *Pulvinulina concentrica*) to Parker and Jones because they had told him that they had already seen, named and illustrated them in a manuscript which was to be read on 12th May 1864 (eventually published 1865). Since Parker & Jones' paper is far longer and more detailed than Brady's, it is reasonable to assume that they had thought up the names at a much earlier date. Brady acknowledges their help in the preparation of his paper (1864: 466), so he was clearly prepared to concede authorship; in these cases, therefore, authorship is quoted as 'Parker & Jones, *in* Brady 1864'.

THE NUMBERING SYSTEM

Register numbers

The British Museum (Natural History) (abbreviated in the text to 'BM(NH)') register numbers for Recent material are variously prefixed 1894:, 1963:, etc., and ZF. The prefix P signifies a fossil. All the specimens are housed in the Micropalaeontology Section of the Department of Palaeontology.

Slide numbers

The fossil and Recent slides are also numbered (in addition to the Museum Register number) with Jones' own numerical reference system within each Catalogue, and this allows the slide to be found quickly. For example XCIV.2, in which the Roman numerals (XCIV) key the locality, the arabic (2) the slide.

THE TYPES OF THE NEW SPECIES

The following section provides information on the type specimens described by Parker, either alone or with colleagues (usually Jones and Brady). Arrangement is alphabetical, giving the type reference, type locality, details of extant material and any necessary remarks. It is unfortunate that, in most cases, it has not been possible to isolate the original figured specimens from the syntypic series. Where lectotypes have been chosen, however, those specimens named in the Catalogue, closest to the original figures, have always been selected. No subjectively identified specimens have been used. Once a type specimen has been selected all other originally cited localities become merely 'localities'.

Several authors – Loeblich & Tappan (1964) for *Discorbina rimosa* and *D. turbo* var. *polystomelloides*, R.W. Jones (1984) for *Lagena sulcata* var. *striatopunctata*, Bolli, Loeblich & Tappan (1957) for *Pullenia obliquiloculata*, Berggren & Kaminski (1990) for *Trochammina squamata* var. *gordialis* and Gibson *et al.* (1991) for *Textularia (Bigenerina) tubulifera* – have all previously selected what they called 'lectotypes' from the Parker Collection from among specimens that were not in fact syntypes, the original syntype series being lost or unrecognized. The selections are, however, tantamount to designating neotypes as I here regard them. Unfortunately, all so-called 'paralectotypes' of these species are without status in taxonomy.

Anomalina coronata Parker & Jones, 1857
Pl. 1, figs 1–3

LECTOTYPE (here designated). From Norway, locality II (*ex* 1894:4:3:216), ZF4913.

TYPE REFERENCE. Parker & Jones 1857: 294; pl. 10, figs 15, 16.

LOCALITIES. Recent specimens were recorded from localities I, II, IV, VII and VIII, along the Norwegian coast; material now only exists from localities II (XXVI), 1894:4:3:216; IV (XXVI.2), 1894:4:3:219 and VIII (XXVI.2), 1894:4:3:227. There are no other specimens extant in the Parker Collection. See pages 38, 39, 41, 113, 124 of Jones' Catalogue.

REMARKS. This species can still be assigned to the Anomalinidae of Cushman. Loeblich & Tappan (1988: 604) synonymize the family with the Alfredinidae of Singh & Kalia, and reject *Anomalina* in favour of *Epistomaroides* Uchio, which would not, in my opinion, contain *A. coronata* since it does not possess the sutural bars and supplementary chambers. Loeblich & Tappan's decision, however, has proved premature as an application to the Commission on Zoological Nomenclature, by Hansen & Rogl (1980), for the suppression of *Anomalina* (on which it depends) has now been withdrawn (see Haynes, 1990: 528). Barker (1960: pl. 97, figs 1, 2) refers the species to *Paromalina* Loeblich & Tappan, and indeed it has been figured by Kihle & Løfaldli (undated circa 1975) as *Paromalina*, from the Norwegian shelf where it has a stratigraphic range of Pleistocene to Recent. *Paromalina* has since been placed in *Discanomalina* Asano by Loeblich & Tappan (1988: 637). Medioli & Scott (1978), in their study of *Discanomalina* in an area off Nova Scotia, concluded that the species *biserialis, coronata, semipunctata* and *japonica* intergrade; thus *coronata* becomes a subjective junior synonym of *semipunctata* (Bailey) with a stratigraphic range of Miocene to Recent.

Articulina multilocularis Brady, Parker & Jones, 1888
Pl. 1, figs 4, 7. Fig. 1.1

LECTOTYPE (here designated). From Plumper station 2 (*ex* 1894:4:3:1033), ZF4914.

TYPE REFERENCE. Brady, Parker, & Jones 1888: 212; pl. 40, fig. 10.

TYPE LOCALITY. Recent, fragments of nullipore, H.M.S. Plumper station 2, in 31 fathoms over Abrolhos Bank, 19°47′S 37°58′W, sounding with some fine sand, off coast of Brazil.

REMARKS. This species is not recorded in Jones' Catalogue (p. 146), but I found a specimen in the Parker Collection

(LXXXV.9) 1894:4:3:1033 from the Abrolhos Bank, in 31 fathoms, which I have designated lectotype and figured here. From the type description it is unclear, but possible, that only one specimen was found. The original figure shows more chambers than my lectotype, but allowing for a degree of artistic licence, it could be argued that they are one and the same and that my lectotype should be more properly referred to as the holotype.

Pearcy (1914) does not record this species from a sample gathered from the type area.

Discorbina biconcava Parker & Jones, *in* Carpenter 1862

LECTOTYPE. Designated by Loeblich & Tappan (1964), ZF3646.

TYPE REFERENCES. Carpenter *et al.* 1862: 202, text-fig. 32g (p. 201); also Parker & Jones, 1865: pl. 19, fig. 10a–c.

TYPE LOCALITY. Recent, shore sand, Melbourne, Australia.

REMARKS. Recorded in the Recent Catalogue, p. 219 (CII.1), 1894:4:3:1520. A lectotype was designated, but not figured, by Loeblich & Tappan (1964: C584). It (ZF3646), and the two paralectotypes (ZF3645) have been re-registered from a slide labelled 'Melbourne'.

D. biconcava is the type species of *Planulinoides* Parr. Barker (1960: pl. 91, fig. 2), refers the species to *Discorbinella* Cushman & Martin.

Discorbina dimidiata Parker & Jones, *in* Carpenter 1862

LECTOTYPE. Designated by Loeblich & Tappan (1964), ZF3651.

TYPE REFERENCES. Carpenter *et al.* 1862: 201, text-fig. 32b (p. 201); also Parker & Jones: 1865: pl. 19, fig. 9a–c.

TYPE LOCALITY. Recent, coast of Melbourne, Australia.

REMARKS. Recorded in Recent Catalogue, p. 219 (CII.2), 1894:4:3:1521, on a slide labelled 'Melbourne'. It is said by Parr (1932: 229) to be very common south of Sydney, Australia. A lectotype (ZF3651) was designated by Loeblich & Tappan (1964: C580) but was unfigured by them; their figured paralectotypes (1964: fig. 456.5–6), which constituted part of an exchange with the BM(NH), are in the U.S. National Museum of Natural History (Smithsonian Institution). The remaining specimens are in the BM(NH) and registered ZF3650.

Loeblich & Tappan (1964: 580) regard *D. dimidiata* as type species of *Lamellodiscorbis* Bermúdez, but later (1988: 559) they placed this genus, without comment, into *Trochulina* d'Orbigny.

Discorbina rimosa Parker & Jones, *in* Carpenter 1862

NEOTYPE. The so-called 'lectotype,' selected by Loeblich & Tappan 1964, is in fact the neotype, P41670: see p. 48. The 'paralectotypes' (see below) have no status as types. For locality see under 'Remarks' below.

TYPE REFERENCE. Carpenter *et al.* 1862: 205.

TYPE FIGURE. *In* Parker & Jones 1865: pl. 19, fig. 6a–c.

LOCALITIES. Fossil, Tertiary: Grignon, France. Recent: Australian coral reefs.

REMARKS. There are no specimens listed in the Catalogues from the original localities. My re-examination of all Grignon and Australian reef slides failed to find any specimens. It is recorded in the Fossil Catalogue (pp. 92, 94) only from 'Hauteville' (Hautteville), Departement Manche, France (LXXIX.40, 43(?) P47227, P47230; also 73–75 see below), collected by Lyell, and in the Recent Catalogue (pp. 206, 207 and 218, XCIII 45–48 and C.8) 1894:4:3:1373–6 and 1517. Loeblich & Tappan (1964: C592–594) designated a 'lectotype' (P41670), as yet unfigured, and 'paralectotypes' (P41669) from the non-topotypic locality at 'Hauteville', France (LXXIX.73–75). The former should properly be a called the 'neotype' (see p. 48), and is formally designated as such herein to stabilize the nomenclature, as the species is type of the genus *Epistomaria* Galloway. The two figured 'paralectotypes' (Loeblich & Tappan 1964: fig. 472.1, 2) are from a suite of six specimens exchanged with the U.S. National Museum of Natural History (Smithsonian Institution).

This species is widely recorded from localities in the Paris Basin by Le Calvez (1970: 153; pl. 32, figs 1–3).

Discorbina turbo (d'Orbigny) var. *globigerinoides* Parker & Jones, 1865

LECTOTYPE. Designated by Loeblich & Tappan 1964, P41661. Grignon.

TYPE REFERENCE. Parker & Jones 1865: 385–6, 421; pl. 19, fig. 7a–c.

LOCALITIES. Fossil, from the Cretaceous (locality unspecified) and Eocene, Calcaire Grossier at Grignon, Paris Basin, France.

REMARKS. It is the type species of *Neocribrella* Cushman. A lectotype and paralectotypes were designated by Loeblich & Tappan from Grignon (1964: C680), respectively registered P41661 and P41660 (probably both from LXXXIV.125 *ex* P47723, as this slide no longer contains specimens); see Fossil Catalogue, p. 105. There are additional specimens (from LXXXIV.96–98) registered P47694–6. Le Calvez (1970: 177; pl. 42, figs 2, 6) records its distribution in the Lutetian of the Paris Basin.

Discorbina turbo (d'Orbigny) var. *polystomelloides* Parker & Jones, 1865

NEOTYPE. The so-called 'lectotype' from Jukes' dredging no. 2, selected by Loeblich & Tappan 1964, is in fact the neotype, ZF3603; see p. 48. The 'paralectotypes' (see below) have no type status.

TYPE REFERENCE. Parker & Jones 1865: 421; pl. 19, fig. 8a–c.

TYPE LOCALITY. From the Recent coral reef, Jukes' dredging (Jukes' no. 2), August 6th 1844, 17 fathoms, white shelly mud, Australia.

REMARKS. The only reference to this species (as *Discorbina polystomelloides*) occurs in the Recent Catalogue, p. 235. It is not from the type locality but from Jukes' dredging No 2, 14 fathoms (CX.20), probably from near (south of) Raine Islet. In the absence of syntypes, Loeblich & Tappan (1964: C594) designated, but did not figure, a 'lectotype' (properly neotype, ZF3603) from this slide. As this species is the type of *Epistomaroides* Uchio, this specimen is formally designated neotype herein in order to stabilize the nomenclature; see p. 48.

Evidence that *Anomalina* and *Epistomaroides* are congeneric is put forward by Hansen & Rögl (1980), who maintain that *Anomalina punctulata* d'Orbigny (the type species of the former) may be a badly drawn *Epistomaria punctata* Said (1949: 37), which they claim is an *Epistomaroides*. Although accepted, rather prematurely, by Loeblich & Tappan (1988: 604), Hansen & Rögl's application to the ICZN for the suppression of *Anomalina* d'Orbigny and the placing of its name on the list of invalid zoological names, and the concomitant application to place the genus name *Epistomaroides* Uchio on the list of valid zoological names, have subsequently been withdrawn (see Haynes, 1990: 519, 528). The two genera remain distinct.

Hauerina plicata Parker & Jones, 1865

Pl. 1, figs 5, 6

LECTOTYPE (here designated). From Jukes' dredging no. 1 (*ex* 1894:4:3:1686), ZF4915.

TYPE REFERENCE. Parker & Jones 1865: 437; table 10.

TYPE FIGURE. *In* Carpenter 1862: pl. 6, fig. 35.

TYPE LOCALITY. From the Recent coral reef, Jukes' dredging (Jukes' no. 1), August 6th 1844, 17 fathoms, white shelly mud, N.E. Australia.

REMARKS. This species is not mentioned in the Catalogue, but from its type locality there are 3 incomplete specimens which are conspecific, referred to *Hauerina ornatissima* Karrer (originally described as *Quinqueloculina*) by Jones; they are from the Jukes' no. 1 dredging (CIX.25), 1894:4:3:1686. In the absence of a good original description of *plicata*, and as the only diagnosis we possess is from its synonym, *Hauerina* sp. of Carpenter (1862: 81; pl. 6, fig. 35), the differences between these two species could be easily overlooked when examined superficially. Karrer's *Q. ornatissima* is fossil, however, so these specimens determined as such by Jones could well be *plicata*, which is only known from the Recent, a fact not considered by Brady (1884: 192). Since the best specimen is so like Carpenter's figure, I have no hesitation in designating it the lectotype. If the two species are subsequently found to be conspecific the name *plicata*, which has not to my knowledge been used recently, would have priority over *ornatissima*. There are no *Hauerina* listed in Murray & Taplin's unpublished Catalogue (1983) of the Carpenter Collection.

Hippocrepina indivisa Parker, *in* Dawson 1870

Pl. 1, figs 8–10

LECTOTYPE (here designated). From Gaspé Bay, 16 fathoms (*ex* 1894:4:3:812), ZF4916.

TYPE REFERENCE. Dawson 1870: 177, text-fig. 2.

LOCALITIES. Recent, from Gaspé Bay; 16 fathoms, also 18–20 fathoms; Gulf of St Lawrence, Canada.

REMARKS. Jones' Catalogue, p. 126 (LXV.2, 6) 1894:4:3:808 and 812, records specimens given to Parker by G.M. Dawson from 16 fathoms only; there are none from 18–20 fathoms. Were H.B. Brady's specimens (1884: pl. 26, figs 10–14) also supplied by Parker? Few of the nine specimens are in good condition; the best show external annular rings without matching internal partitions. The agglutinated wall is of the trochamminaceous type (J.E. Whittaker, personal communication).

H. indivisa (the type species of *Hippocrepina*) still lives in Canadian waters (Schafer & Cole 1978: pl. 1, fig. 8).

Lagena crenata Parker & Jones, 1865

Pl. 1, figs 14, 15

LECTOTYPE (here designated). From Malaga (*ex* P47925), P52783.

TYPE REFERENCE. Parker & Jones 1865: 420; pl. 18, fig. 4a, b.

LOCALITIES. Fossil, of Middle Tertiary age, Bordeaux, France and Malaga, Spain. Recent, from the Swan River shore sand, Australia.

REMARKS. The only extant fossil syntypes are from the Miocene (?) of Malaga (Catalogue: 124, CX.8), P47925; one, selected here as lectotype, is most like Parker & Jones' original figure (although the base is slightly damaged). The only record in the Recent Catalogue (p. 219), from anchor mud, 6–7 fathoms in the Swan River, (XCIX.4), 1894:4:3:1503, does not precisely match the details of the locality as originally given. The species is said to be still commonly found along the south-western coast of Australia (Albani & Yassini 1989: 377).

Lagena distoma Parker & Jones, *in* Brady 1864

Pl. 1, figs 12, 13

LECTOTYPE (here designated). From Norway (*ex* 1894:4:3:230), ZF4917.

TYPE REFERENCE. Brady 1864: 467; pl. 48, fig. 6.

LOCALITIES. Sub-fossil, from the fens near Peterborough, England. Recent, along the coast of Norway, the Shetland Islands (82 fathoms) and the coast of Northumberland, England.

REMARKS. This species was first cited, as *Lagena laevis* (Walker & Montagu) var. *striata* (Montagu), by Parker & Jones, 1857: pl. 11, fig. 24 from the Norway Recent (top paragraph, p. 283), where it is still found (Kihle & Løfaldli [undated, circa 1975]). There are sub-fossil specimens from sandy clay alluvium, on the border of Cambridgeshire and Huntingdonshire, Peterborough Fen, one mile from its western boundary, (CXL.38–40), P48441–3, Catalogue p. 167. There is one specimen from Shetland (Catalogue p. 21, XXII.3), 1894:4:3:129 and one specimen from the Norway locality VIII, 30–200 fathoms (Catalogue: 40, 41, XXVI.5), 1894:4:3:230. My lectotype from this last-named locality is most like the original figured specimen. The sub-fossil preparations are balsam strews and no specimens are visible on P48441 (CXL.38) or P48442 (CLX.39).

The authorship of *distoma* was cited by Brady, 1864 as 'Parker and Jones MS' (see p. 48). R.W. Jones (1984: 125) placed this species into his own subfamily the Phialineiinae and new genus *Phialinea,* but now (personal communication) prefers to refer it to *Procerolagena* Puri (a senior synonym of

Hyalinonetrion Patterson & Richardson). He regards *Lagena gracilis* Williamson, 1848 (the type-species by original designation of *Procerolagena*) as arguably a senior synonym of *Lagena distoma* Parker & Jones, *in* Brady 1884: 461.

Lagena sulcata (Walker & Jacob) var. ***distomaaculeata*** Parker & Jones, 1865

TYPE REFERENCE. Parker & Jones 1865: 348, 420; pl. 18, fig. 5 (as *distoma-aculeata*)

TYPE LOCALITY. Fossil, from the Tertiary, Eocene, Calcaire Grossier at Grignon (in the Paris basin).

REMARKS. There are Catalogue records of *L. sulcata* from the Eocene, Calcaire Grossier of Grignon, France (LXXXIV.59, 60), P47659–60, but these are not var. *distomaaculeata*. As there are no records in the Catalogue under *aculeata*, *distoma*, *distoma-aculeata* or *sulcata* varieties, and a search of all the Grignon slides has revealed nothing, it must be assumed that these rare specimens have been lost.

Lagena sulcata (Walker & Jacob) var. ***distomamargaritifera*** Parker & Jones, 1865

?Pl. 1, figs 20, 21

TYPE REFERENCE. Parker & Jones 1865: 348, 357; pl. 18, fig. 6a, b (as *distoma-margaritifera*).

TYPE LOCALITY. Recent, sponge sand ('surf-washed sponges' in plate explanation), from Melbourne, Australia.

REMARKS. Not recorded in the Catalogue under its full original name, it can be found neither under *L. margaritifera* nor *distoma-margaritifera*. There is, however, a record of *Lagena distoma* from Melbourne shore sand, Australia, (CII.2), 1894:4:3:1521 (4th specimen from left) which is not typical of that species (compare with illustration of *Lagena distoma* above), and is illustrated here. The original figured specimen (pl. 18, fig. 6a) (the description reads as if there was more than one specimen) was ornamented with 'pearl like grains'). My illustrated specimen (ZF4918) bears elongate raised bars, some anastomosing, and is similar to the two specimens figured by Albani & Yassini (1989: 381, figs 3B, C) as *Procerolagena distoma margaritifera* from Port Stephens, eastern Australia. Even though this is the only specimen extant in the Parker Collection which shows any similarity to the type illustration, it differs enough in ornament to make the designation of a lectotype unwise without knowing the range of variation; furthermore, it is not clear whether it is strictly a syntype. There are records from Melbourne of *Lagena sulcata s.s.* (CII.1) 1894:4:3:1520 (this has randomly arranged pits) and *L. sulcata* ? (CIII.I) 1894:4:3:1569, which are not conspecific.

The genus *Procerolagena* Puri was considered synonymous with *Lagena* by Loeblich & Tappan (1964: C518) but was reinstated (1988 : 416) without explanation (see also discussion under *Lagena distoma*, p. 50).

Lagena sulcata (Walker & Jacob) var. ***distomapolita*** Parker & Jones, 1865

Pl. 1, fig. 22

LECTOTYPE (here designated). From Jukes dredging no. 1, N.E. Australia (*ex* 1894:4:3:1686), ZF4919.

TYPE REFERENCE. Parker & Jones 1865: 357; pl. 13, fig. 21 and pl. 18, fig. 8 (as *distoma-polita*).

LOCALITIES. Fossil, Crag of Suffolk, England. Recent, Norway dredgings, 30–200 fathoms between North Cape and Drontheim, from 69° to 63°N (Norway locality VIII); Red Sea, in the Gulf of Suez (No. 1 of Pullen's MS list) a light yellow (ochreous) clay, close to Island Shadwan off S.E. point entrance of Jubal Strait, 372 fathoms; coast sand, 7 or 8 fathoms, Swan River, Melbourne, Australia; Jukes' dredging (no. 1, August 6th 1844), 17 fathoms, a white shelly mud near Raine Islet, 11°30′S 144°E, northern part of the Great Barrier Reef; on the Durham coast, England.

REMARKS. The records of *Lagena polita* (Catalogue, p. 165) from the Pleistocene, Valley of the Nene, Wisbeach [a misspelling of Wisbech, Cambridgeshire] (CXXXVII.2) P48400 and Pleistocene, Boston, Lincolnshire, eastern England (CXXXVIII.1) P48401 are misidentifications. Though never recorded under its full varietal name but as *Lagena distomapolita* (Recent Catalogue), it is possible that the specimen illustrated on pl. 13, fig. 21 of Parker & Jones, 1865 is that from the Norway locality VIII (XXVI.24) 1894:4:3:249, since in the type description the word 'Arctic' is written after the figure number. It is the correct size and the Catalogue (p. 43) refers to this figure, but it is not clear whether Jones is making a comparison or a definite statement of fact. Jones obviously had a problem in distinguishing *distomapolita* from *Amphorina gracillima* Seguenzæ, 1862 (*gracillima* has a more rounded fusiform side view), for it is recorded as the latter from Jukes' dredging no. 1 (Catalogue p. 230, XIX.25) 1894:4:3:1686; it is from this slide that a lectotype has been chosen as it compares favourably with the specimen in pl. 18, fig. 8 of the original figures. There are other specimens from the Red Sea (LXXXIX.3) 1894:4:3:1085, not listed in the Recent Catalogue, p. 157. The Jukes' dredgings come from an area which was extensively recollected by H.M.S. Challenger (see co-ordinates given above). The specimens in the Parker Collection from Melbourne (CII.1, 2) 1892:4:3:1520, 1521, I consider to be *gracillima*. Jones does not list 'on the Durham coast' in his Catalogue, and there are no specimens in the Dogger Bank slides (XVIII and XIX) 1894:4:3:122–124; there are however specimens labelled *gracillima* from this area in Brady's BM(NH) collection, which need fuller investigation. The fossil record from Sutton, listed as *gracillima,* (CXXX.22) P48311, is indeed that species. Whittaker & Hodgkinson (1979: 43) considered that specimens similar to those of Parker & Jones (1865: pl. 18, fig. 8) formed part of a series which could be referred to *Lagena clavata* d'Orbigny.

The species *distomapolita* was placed by Albani & Yassini 1989 into *Procerolagena* Puri (see remarks above, under *Lagena sulcata* var. *distomamargaritifera*).

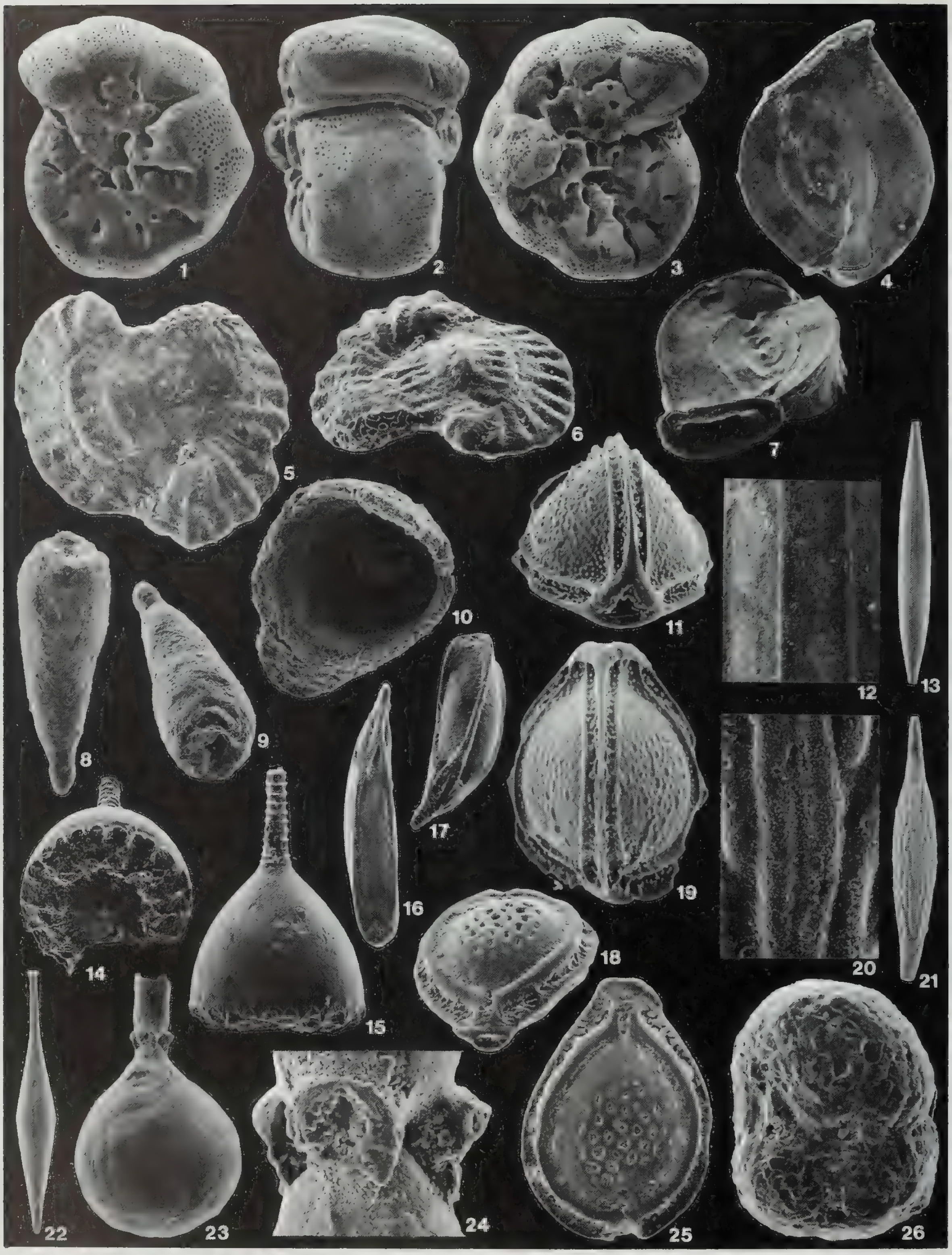
Lagena sulcata (Walker & Jacob) var. ***marginata*** (Montagu) subvar. ***squamosomarginata*** Parker & Jones, 1865

Pl. 1, figs 18, 25; Fig. 1.2

LECTOTYPE (here designated). From Jukes' dredging no. 1, N.E. Australia (*ex* 1894:4:3:1686), ZF4920.

TYPE REFERENCE. Parker & Jones 1865: 348, 356; pl. 18, fig. 2a, b (as *squamoso-marginata*).

LOCALITIES. Fossil, in the Middle Tertiary beds of San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Domingo. Recent, living on the coral-reefs of Australia (Jukes).

REMARKS. The *Lagena sulcata* group from the Middle Tertiary of San Domingo is not recorded in the Catalogue. There is, however, a single specimen from Jukes' dredging (no. 1, August 6th 1844), 17 fathoms, white shelly mud near Raine Islet, 11°30′S, 114°E, northern part of the Great Barrier Reef); it is labelled '*Lagena squamosomarginata* ?' (Catalogue p. 230, CIX.25) 1894:4:3:1686. I have designated this as lectotype. It has a slit-like aperture and 'entosolenian' tube ('endosolen' of Knight, 1986), which would place it in the Ellipsolageninae of Silvestri (Loeblich & Tappan 1988: 428); the presence of a short neck, non-radiate aperture, endosolon and peripheral keels, and absence of a phialine lip indicate the genus *Lagenosolenia* McCulloch (Loeblich & Tappan 1988: 428). Barker (1960: pl. 60, fig. 24) raised *squamosomarginata* to specific level within *Fissurina* Reuss.

Lagena sulcata (Walker & Jacob) var. ***striatopunctata*** Parker & Jones, 1865

NEOTYPE. The so-called 'lectotype' selected by R.W. Jones, 1984, is in fact the neotype: see p. 48.

TYPE REFERENCE. Parker & Jones, 1865: 350; pl. 13, figs 25–27.

LOCALITIES. Fossil, Eocene deposits of Grignon, France, inside a shell (although the species is not figured from this locality the note in the type reference, 1865: 419, may mean that this was one of the species found within the *Cerithium giganteum*). Recent, Indian Ocean on a clam shell and at 2200 fathoms, a fine white calcareous mud with Polycystinae, 5°37′S 61°33′E; the Red Sea at 372 fathoms, a light yellow clay, close to Island Shadwan, off SE point at entrance of Jubal Strait; the South Atlantic at 2700 fathoms, pale mud, half aluminous, 26°45′S 32°52′W; the Hunde Islands at 30–40 fathoms, in 'South-east or Disco Bay', Davis Straits, west coast of Greenland, 68°50′W 53°N.

REMARKS. There are no syntypes. No fossil specimens have been found. The Recent Catalogue (pp. 10, 30) refers only to *Lagena striatopunctata*. The type figures were of specimens from the Arctic (west coast of Greenland) Hunde Islands, No. 3, 30–40 fathoms, with a shelly sandy mud bottom, a sample not mentioned in Jones' Catalogue. R.W. Jones' 'lectotype' (ZF3416) is from the Hunde Islands No. 2, 28–30 fathoms (Catalogue : 30, XXV.2c) 1894:4:3:175, with a 'gravel bottom'. Since it is not in fact a syntype his specimen is here referred to as the neotype (p. 48).

The perforations on the ribs suggest this form should be included within the genus *Cushmanina* R.W. Jones (1984: 105). Barker (1960: pl. 58, figs 37–40) raised the taxon to specific level within *Oolina*. Le Calvez (1970: 82; pl. 16, fig. 1), as *Lagena*, records it from the Lutetian of Montjavoult (south of Gisors) in the Paris basin, but not from Grignon.

Lagena sulcata (Walker & Jacob) var. ***tetragona*** Parker & Jones, 1865

Pl. 1, figs 16, 17

LECTOTYPE (here designated). From Grignon (*ex* P47660), P52784.

TYPE REFERENCE. Parker & Jones 1865: 352, 420; pl. 18, fig. 14a, b.

TYPE LOCALITY. Eocene, the Calcaire Grossier; Grignon, France.

REMARKS. Recorded as *Lagena tetragona* (slides LXXXIV.59–61), P47659–61 from the Calcaire Grossier of the Paris Basin, Grignon, near Paris; one of the best specimens is made lectotype. The 'ridges/spiral ribs' in the neck

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PLATE 1

Figs 1–3 *Anomalina coronata* Parker & Jones. Lectotype ZF4913, here designated; Norway. Dorsal, edge and ventral views, respectively. All × 40.

Figs 4, 7 *Articulina multilocularis* Brady, Parker & Jones. Lectotype ZF4914, here designated; Abrolhos Bank. Side and oblique apertural views, × 125. See also Fig. 1.1 (p. 56).

Figs 5, 6 *Hauerina plicata* Parker & Jones. Lectotype ZF4915, here designated; N.E. Australia. Side and oblique-apertural views, × 95.

Figs 8–10 *Hippocrepina indivisa* Parker. Figs 8, 9, Lectotype ZF4916, here designated; Gaspé Bay. Side and oblique apertural view, × 45; Fig. 10, Paralectotype ZF4916a, broken specimen from same locality, view showing lack of internal structures, × 130.

Figs 11, 19 *Lagena sulcata* (Walker & Jacob) var. *trigonomarginata* Parker & Jones. P52785, from the Eocene of Grignon, France; oblique-apertural and side views, respectively. Both views showing the three ribs on a single margin only, × 195.

Figs 12, 13 *Lagena distoma* Parker & Jones. Lectotype ZF4917, here designated; Norway. Fig. 12, detail of ornament, × 395; Fig. 13, entire specimen, × 40.

Figs 14, 15 *Lagena crenata* Parker & Jones. Lectotype P52783, here designated; Middle Tertiary, Malaga. Basal and side views, respectively, × 100.

Figs 16, 17 *Lagena sulcata* (Walker & Jacob) var. *tetragona* Parker & Jones. Lectotype P52784, here designated; Calcaire Grossier, Grignon. Side and oblique-apertural views, respectively, × 135.

Figs 18, 25 *Lagena sulcata* (Walker & Jacob) var. *marginata* (Montagu) subvar. *squamosomarginata* Parker & Jones. Lectotype ZF4920, here designated; N.E. Australia. Oblique-apertural and side views, respectively, × 160. See also Fig. 1.2 (p. 56).

Figs 20, 21 Possibly *Lagena sulcata* (Walker & Jacob) var. *distomamargaritifera* Parker & Jones. ZF4918, from sponge sand, Melbourne, Australia. Fig. 20, detail of ornament, × 300; Fig. 21, entire specimen, × 40. See text p. 51.

Fig. 22 *Lagena sulcata* (Walker & Jacob) var. *distomapolita* Parker & Jones. Lectotype ZF4919, here designated; N.E. Australia. Side view, × 40.

Figs. 23, 24 *Lagena sulcata* (Walker & Jacob) var. *tubiferosquamosa* Parker & Jones. Lectotype P52786, here designated; Calcaire Grossier, Grignon. Fig. 23, side view, × 75; Fig. 24, detail of 'tubes' on neck, × 400.

Fig. 26 *Lituola nautiloidea* Lamarck var. *globigeriniformis* Parker & Jones. Lectotype ZF3658; north of Newfoundland Bank. Ventral view, × 330.

All scanning electron photomicrographs.

region can fork and recombine. If Le Calvez, 1970, ever observed this species from Grignon she did not record it.

Lagena sulcata (Walker & Jacob) var. ***trigonomarginata*** Parker & Jones, 1865

Pl. 1, figs 11, 19

TYPE REFERENCE. Parker & Jones 1865: 348, 352, 419; pl. 18, fig. 1a, b (as *trigono-marginata*).

TYPE LOCALITY. Eocene, from inside a *Cerithium giganteum* shell, Calcaire Grossier; Grignon, France (Parker & Jones 1865: 419, note).

REMARKS. Recorded as *Lagena trigonomarginata* in the Recent Catalogue (p. 10) from Skye and Whitehaven, but not from Grignon (Fossil Catalogue, p.100–107). There is a *marginata* (Mont.) mentioned on p. 103, (LXXXIV.57, 58) P47657–8, but the specimens so called are not conspecific since they lack the 'three, meridional, three-edged equal ribs'. P47656–67 and P47724 (LXXXIV.56–67 and 126), which should have contained *sulcata* and/or *marginata*, in fact did not. From slide LXXXIV.61 (P47661) a specimen with three ribs in one plane only, but bi-ribbed in the other two planes, has been isolated, re-registered P52785 and illustrated here. Parker & Jones' figured specimen has not been found; I suspect that the number of ribs is variable. No lectotype is designated.

The taxon may well belong in *Galwayella* Patterson & Richardson.

Lagena sulcata (Walker & Jacob) var. ***tubiferosquamosa*** Parker & Jones, 1865

Pl. 1, figs 23, 24

LECTOTYPE (here designated). From Grignon (*ex* P47669), P52786.

TYPE REFERENCE. Parker & Jones 1865: 354, 420; pl. 18, fig. 7a, b (as *tubifero-squamosa)*.

TYPE LOCALITY. Eocene, from inside a *Cerithium giganteum* shell, Calcaire Grossier; Grignon, France (Parker & Jones 1865: 419, note).

REMARKS. Referred to as *tubuliferosquamosa* (a mis-spelling by Jones) in the fossil Catalogue (pp. 103, 107, LXXXIV.68–72, 126), P47725, P47668–72, from Grignon. The figured specimen has not been isolated and would be difficult to recognize with certainty. The specimens on slide LXXXIV.126 have been remounted (P47725). There are numerous, mostly worn and poorly preserved, specimens on slides 68 (P47668) and 69 (P47669); few have the characteristic neck, which might account for Le Calvez' (1970) failure to report them. One of the most complete individuals on slide P47669 has been designated lectotype. This species is unlike any lagenid I have seen and possibly not even a foraminifer.

Lituola cassis Parker, *in* Dawson 1870

Figs 2.1, 2

LECTOTYPE (here designated). From Gaspé Bay (*ex* 1894:4:3:813), ZF4637.

TYPE REFERENCE. Dawson 1870: 177, text-fig. 3.

TYPE LOCALITY. Recent, from Gaspé Bay, between 10–17 fathoms; Gulf of St Lawrence, Canada.

REMARKS. There are syntypes recorded as *Haplophragmium cassis* (Catalogue p. 126, LXV.3) 1894:4:3:809 and a strew (LXV.7) 1894:4:3:813 with several specimens. This large species is under fuller investigation by Brönnimann & Whittaker (in preparation), on whose advise a lectotype has been chosen. It is the type species of *Ammotium* Loeblich & Tappan and still lives in the type area (Schafer & Cole 1978).

Lituola findens Parker, *in* Dawson 1870

LECTOTYPE (here designated). From Gaspé Bay (*ex* 1894:4:3:810), ZF4929.

TYPE REFERENCE. Dawson 1870: 176; text-fig. 1 (p. 177).

LOCALITIES. Recent, from Gaspé Bay, 16–20 fathoms; and St George's Cove in Gaspé Bay; Gulf of St Lawrence, Canada.

REMARKS. Recorded as *Reophax findens* (Catalogue p. 126, LXV.4) 1894:4:3:810. Of the specimens in the collection, only one could possibly have been a figured specimen (centre drawing of text-fig. 1) and is here designated lectotype; because it is broken and extremely fragile it is not re-illustrated here, nor is it separated from the accompanying specimens. There are no syntypes from St George's Cove, but topotypes of *Reophax findens* (Parker) are present in the Heron-Allen and Earland Students Collection, BM(NH). Loeblich & Tappan (1988: pl. 47, figs 7–10) reillustrate Brady's *Challenger* specimens of *Reophax findens* from Gaspé Bay, 18–20 fathoms (1884: pl. 32, figs 10a, b and 11a, b), BM(NH) ZF2272.

Lituola findens is the type species of *Protoschista* Eimer & Fickert.

Lituola nautiloidea Lamarck var. ***globigeriniformis*** Parker & Jones, 1865

Pl. 1, fig. 26

LECTOTYPE. From north of the Newfoundland Bank, ZF3658. Designated by Loeblich & Tappan, 1964.

TYPE REFERENCE. Parker & Jones 1865: 407; pl. 15, figs 46, 47 (Arctic) and pl. 17, figs 96–98 (North Atlantic).

TYPE LOCALITIES. Recent. 30–70 fathoms at Hunde Islands, in South-east or Disco Bay, Davis Straits, west coast of Greenland (68°50′W 53°N); from Baffin's Bay, depth not recorded (75°10′N 60°12′W); also at 314 fathoms (75°25′N 60°W) and 220 fathoms (75°N 59°40′W); in the Boreal tract towards Newfoundland Bank, 1660 fathoms (51°30′N 38°W); from the north of Newfoundland Bank at 145 and 954 fathoms, North Atlantic Ocean; in the Red Sea, 557 fathoms, (17°49′N 40°02′E) and 678 fathoms (23°30′N 36°58′E); from the Abrolhos Bank in the South Atlantic at 260 fathoms (22°45′S 40°37′W) and 940 fathoms (19°32′S 37°51.5′W); from the Indian Ocean, 2200 fathoms (5°37′S 61°33′E); and the Mediterranean sea (no details given).

REMARKS. The lectotype selected and figured by Loeblich & Tappan (1964: C259, fig. 173:2a–c) is that figured by Parker & Jones (1865: pl. 17, fig. 96) from the North Atlantic (*ex* 1894:4:3:294), ZF3658. It is from a locality at 49°23′N 48°48′W, 954 fathoms, Arctic, north of Newfoundland Bank, as given in Table 5 of the type reference, but not quoted in full in the Ellis & Messina Catalogue.

L. nautiloidea var. *globigeriniformis* (as *Ammoglobigerina* *bulloides* Eimer & Fickert) is the type species of *Ammoglobigerina* Eimer & Fickert which was regarded as synonymous with *Trochammina* Parker & Jones by Loeblich & Tappan (1964: C259). In Loeblich & Tappan (1988: 120) both genera are, however, recognized. The lectotype was reillustrated by Brönnimann & Whittaker (1988: 37–38, figs 20I–K), who concluded that the generic affinities of *Ammoglobigerina* could not be properly ascertained and that both the species and genus should be considered *nomina dubia*. The lectotype is refigured here in umbilical view, after cleaning, to show that the apertural characters are not visible.

All records in the Recent Catalogue of *Haplophragmium globigeriniforme* from Baffin's Bay (p. 26) 75°10′N 60°12′W, and (p. 27) 75°55′N 60°W, 314 fathoms, gathered during Sir Edward Parry's Expedition to the Arctic, (XXIV.1, 6) 1894:4:3:157 & 164, should be referred to *Adercotryma glomeratum* (Brady), 1878 (formerly *Lituola*). So also should those from the Newfoundland bank area (material from Dayman's H.M.S. Cyclops gatherings), (XXVII.31) 1894:4:3:294 (J.E. Whittaker, personal communication).

Lituola nautiloidea Lamarck var. ***soldanii*** Jones & Parker, 1860

Pl. 2, figs 1–3

Lectotype (here designated). From Miocene of San Domingo (*ex* P48099), P52787.

Type reference. Jones & Parker 1860: 307; no figure.

Localities. Fossil; Miocene, sandy clay of San Domingo, and Pliocene, Tejares clay of Malaga. Recent, Victoria Bank (Abrolhos Bank) off Brazil.

Remarks. Specimens from Jamaica, listed in the Recent Catalogue (p. 140) as *Haplostiche soldanii*, are not syntypes; there is nothing from the Abrolhos Bank (spelt Abrohlos by Jones). There are, however, syntypes listed in the Fossil Catalogue (p. 124) from the Miocene (?) of Malaga, Spain (CX.1) P47918 and (p.129) from the Miocene of San Domingo (CX1.11) P48098, (CXI.12) P48099 and (CX1.13) P48100; an individual from the latter locality is selected as lectotype and figured here. Jones, in the Catalogue, states that we must refer to Soldani's (1798) *Testaceographiae*, **2:** fig. 3/cc and his (1758) *Saggio Orittografico*: pl. 19, 92/z to see the illustrations of this form.

Jones & Parker's taxon is the type species of *Liebusella* Cushman 1933, who reproduced the non-syntypic figure of *Haplostiche soldanii* from Brady (1884: pl. 32, fig. 14 only), a Recent specimen from Challenger station 33, depth 435 fathoms off Bermuda (slide labelled, Bermudas) (ZF1559), and illustrated his own specimens from an unspecified locality.

Miliolina excisa Brady, Parker & Jones, 1888

Type reference. Brady, Parker & Jones, 1888: 215; pl. 40, fig. 33.

Type locality. Recent; a sounding, fragments of nullipore with some fine sand, at Plumper station 2 (19°47′S 37°58′W), 31 fathoms, Victoria Bank (Abrolhos Bank) off the coast of Brazil, South America.

Remarks. This species is not listed in Jones' Recent Catalogue (p. 146), nor are any specimens like it present either at the type locality (LXXXV.9–12) 1894:4:3:1033–36 or in the Brady Collection, BM(NH). Brady did not discuss or illustrate it in the Challenger Report (1884), nor is it recorded by Pearcy, 1914 from his Abrolhos sample. I must assume that there are no specimens extant.

Nodosaria (Marginulina) raphanus (Linnaeus) var. ***falx*** Jones & Parker, 1860

Pl. 2, figs 5, 6

Type reference. Jones & Parker, 1860: 302; no figure.

Type localities. Recent; off Syra in the Grecian Archipelago, 90 fathoms, and from near Crete, 360 fathoms, both in the Mediterranean Sea.

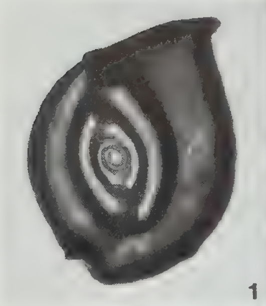
Remarks. In the Catalogue it is recorded as *Amphicoryna falx* from 'near Crete, mud at 360 fathoms', (LVII.5) 1894:4:3:752. There are no specimens from Syra. *Marginulina falx* was designated type species of *Nodosariopsis* Silvestri (*non* Rzehak, 1895) by Loeblich & Tappan (1964: C513–514), but this is an objective synonym of *Amphicoryna,* as *Marginulina falx* was also earlier designated type of *Amphicoryna* Schlumberger (*in* Milne Edwards) by Brady (1884: 556; pl. 65, figs 7–9); see also Loeblich & Tappan (1988: 410). Brady's figures are possibly the first of this species, based on his own interpretation of Jones & Parker's description. Brady considered *falx* to be not a variety of *raphanus* but of *longicauda* d'Orbigny which, as he remarked in his footnote to p. 556, 'is now better known under its earlier name *Nodosaria scalaris* Batsch sp.' (*Nautilus (Orthoceras) scalaris* Batsch, 1791). It is apparent that Loeblich & Tappan (1964: C513), who figure a beautiful specimen from Syra, also consider *falx* to be synonymous with Batsch's species. My researches, however, suggest this may not be the case. *Amphicoryna* (based on its type species *falx*), as diagnosed by Loeblich & Tappan (1988: 410; pl. 450, figs 11–14), has an 'astacoline' initial coil in the microspheric form and, in the megalospheric generation, a large globular proloculus followed by rectilinear globular chambers throughout, features which they do not illustrate. *Nautilus scalaris,* as figured by Batsch, is rectilinear throughout indicating a megalospheric generation, but what is the form of the microspheric generation? My figured specimen (ZF4921) has been examined in clove oil; even though the internal details are still unclear, there is certainly an 'astacoline' coil present, which should be indicative of the microspheric generation. The size of the specimen and number of chambers, however, make this improbable. Closer examination of the initial coil in both *falx* and *scalaris* is required. No lectotype is selected.

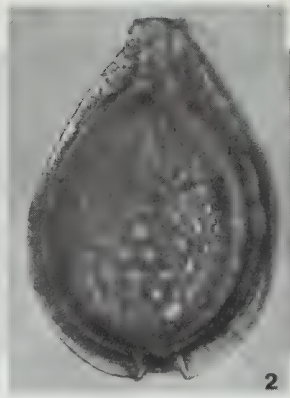
Nonionina exponens Brady, Parker & Jones, 1888

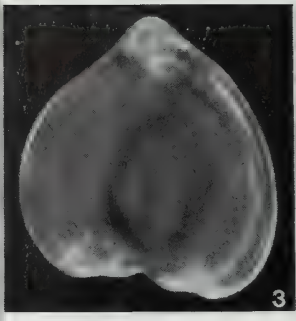
Type reference. Brady, Parker & Jones, 1888: 230; pl. 43, fig. 16a, b.

Type locality. Recent; sounding, whitish mud at 940 fathoms, Plumper station 1, 19°32′S 37°5.5′W, Abrolhos Bank, off coast of Brazil, South Atlantic.

Remarks. Not mentioned in the Catalogue (p. 145). All 8 slides from Plumper station 1, (LXXXV.1–8) 1894:4:3:1025–32, have been examined, but no specimens have yet been found; the supposed record on (LXXXV.3) 1894:4:3:1028 is incorrect. None have been found in Brady's







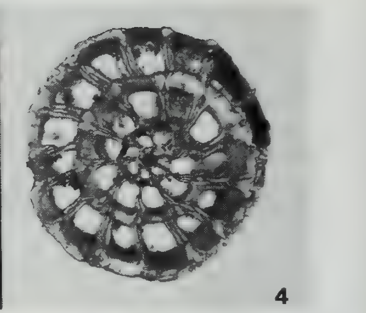


Fig. 1.1 *Articulina multilocularis* Brady, Parker & Jones. Lectotype, ZF4914, here designated; Abrolhos Bank. Clove oil immersion, × 95. See also Pl. 1, figs 4, 7.

Fig. 1.2 *Lagena sulcata* (Walker & Jacob) var. *marginata* (Montagu) subvar. *squamosomarginata* Parker & Jones. Lectotype, ZF4920, here designated; N.E. Australia. Clove oil immersion, showing the endosolon, × 175. See also Pl. 1, figs 18, 25.

Fig. 1.3 *Polymorphina elegantissima* Parker & Jones. Lectotype, 1955:10:3:8, here designated; Storm Bay, Tasmania. Clove oil immersion, × 40. See also Pl. 2, figs 7, 8.

Fig. 1.4 *Rotalia schroeteriana* Parker & Jones. Paralectotype (W.B. Carpenter slide 263/1903-634, in the Royal Albert Memorial Museum, Exeter); Philippines. Equatorial thin section of microspheric form, × 25.

All optical photographs.

collection in the BM(NH), nor was it recorded by Pearcy (1914: 1038).

Nubecularia lucifuga Defrance var. ***tibia*** Jones & Parker, 1860*a*

LECTOTYPE. Designated by Adams (1962), P41672.

TYPE REFERENCE. Jones & Parker, 1860*a*: 455; pl. 20, figs 48–51.

TYPE LOCALITY. Fossil; 'Upper Triassic, blue clay of Messrs Cubitt's alabaster pits, Chellaston, three miles south of Derby, England' (*sic*; see note below).

REMARKS. Recorded in the Fossil Catalogue (p. 5), as *Nubecularia tibia*. The type locality is probably incorrect, since in the Catalogue (entry with VIII.5) Jones writes '. . . Described by mistake as Triassic clay from Chellaston near Derby . . . Probably some Lias clay brought by the same conveyance (canal barge ?) from a place south of Derbyshire, as the Red Clay came (from Chellaston)' (see under *Planularia pauperata*, p. 58). This record was made by Jones some 32 years on, and is confusing and now unverifiable. The lectotype P41672 was designated and illustrated by Adams (1962: 164–165; pl. 23, figs 4, 5 and p. 161, text-fig. 1E) and is deposited in the BM(NH), under *Nubeculinella*.

Nubecularia tibia is the type species of *Nodobacularia* Rhumbler (1895). However, since Adams (1962) considers the type specimen of *tibia* to belong to *Nubeculinella* Cushman and that genus is synonymized by Loeblich & Tappan (1988: 323) with *Vinelloidea* Canu (1913), then the genus *Vinelloidea* should surely be suppressed in favour of *Nodobacularia*; Loeblich & Tappan make no reference to this problem, nor quote Adams (1962) in their references. The findings of Adams (1962) suggest that a re-examination of the generic characters of these four genera is desirable.

Note on *Orbitolina*

Parker & Jones (1860*a*: 37) clearly state that the following are all varieties of *Orbitolina concava* Lamarck, and on p. 29 they express their views on the structure and relationship of the genus from its simplest variety (*Orbitolina simplex*) to its highest state of development, *O. lenticularis*. None of the varieties were illustrated and in many cases the diagnostic features are obscure, but it is clear that the varieties really belong to *Gypsina* and associated genera and are not Orbitolinidae. It is apparent from Jones' Catalogues that, with the limited time available to him, he was unwilling to engage in time-consuming identifications. Having no knowledge of this group of largely unfigured varieties I have not selected lectotypes.

Orbitolina concava Lamarck var. ***annularis*** Parker & Jones, 1860*a*

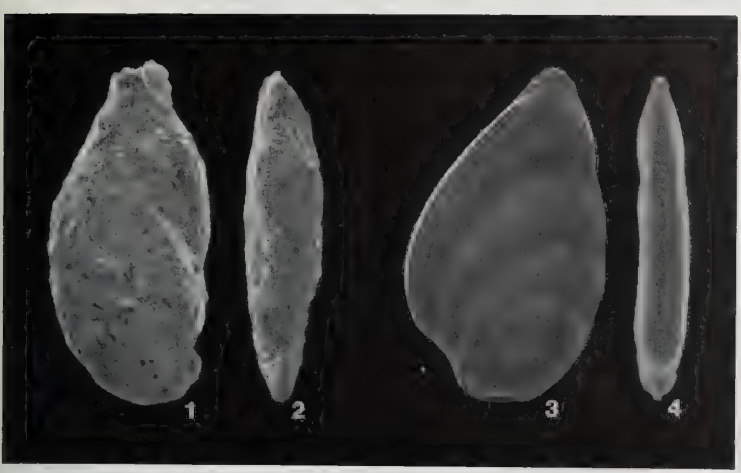
LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3597.

TYPE REFERENCE. Parker & Jones, 1860*a*: 30, 38. No figure.

TYPE LOCALITY. Recent; from Melbourne, Australia.

REMARKS. It is recorded in Jones' Catalogue as *Patellina annularis* on pp. 219, 223, 230, 235, and 245. An unfigured lectotype was designated from CII.2 (ZF3597) by Loeblich & Tappan (1964: C730–1). Their figured specimen (1964: fig. 599.1) is from their own collection. The remaining paralectotypes are in the BM(NH) registered ZF3596 (all *ex* 1894:4:3:1521). There are also other specimens from Melbourne (CIII.60–62) 1894:4:3:1581–3.

P. annularis is the type species of *Annulopatellina* Parr & Collins and is placed by Loeblich & Tappan (1988) in their own Superfamily Annulopatellinacea.



Figs 2.1, 2 *Lituola cassis* Parker. Lectotype, ZF4637, here designated; Gaspé Bay. Side and edge views, × 30.
Figs 2.3, 4 *Planularia pauperata* Jones & Parker. P52792; locality ? (see p. 59). Side and edge views, × 110.
All scanning electron micrographs.

Orbitolina concava Lamarck var. ***congesta*** Parker & Jones, 1860*a*

TYPE REFERENCE. Parker & Jones, 1860*a*: 32, 38. No figure.

TYPE LOCALITY. Recent; from Australia (area unspecified).

REMARKS. Not recorded in the Catalogue under either *congesta* or *concava* var. *congesta*. In the type description it is said to accompany *O. concava* var. *vesicularis*, but it might be difficult to tell these two varieties apart when studying an assemblage and clearly Jones, 30 years on, was unable to do so. Brady (1884: 718) considered *congesta* to be indistinguishable from the loosely defined variety *vesicularis*, which he raised to specific level within the genus *Gypsina*. Further research is necessary to isolate this variety.

Orbitolina concava Lamarck var. ***laevis*** Parker & Jones, 1860*a*

TYPE REFERENCE. Parker & Jones, 1860*a*: 32, 38. No figure.

LOCALITIES. Fossil; from the Tertiary of Palermo, Sicily; Bordeaux, France; and San Domingo, West Indies. Recent; from Australia, Fiji, West and East Indies, Mediterranean Sea, British Coast (as far north as the Isle of Arran).

REMARKS. Jones only records *Gypsina globula*, not *laevis*, from the Pliocene of Palermo (Sicily) (p. 136, CXV.32) P48194 and from the Miocene of San Domingo, (CXI.14, 15, 24, 25) P48101–2, P48111–2. In the Recent Catalogue *Gypsina laevis* is listed from the British coast, the Dogger Bank (p. 19, XVIII.11) 1894:4:3:123 and off Northumberland ('Alnwick and Dogger'), (p. 20, XX.1) 1894:4:3:124. None of these specimens is spherical or bears any resemblance to *Gypsina*, as represented by the group including the varieties *congesta* and *vesicularis*, so I can only assume that Jones misidentified the English specimens. Later called *Tinoporus laevis* by Parker & Jones (1865: 434, table 10 for column No. 7). There are no other records in either Catalogue, under any genus I could find, of *concava* or *laevis*.

Orbitolina concava Lamarck var. ***semiannularis*** Parker & Jones, 1860*a*

TYPE REFERENCE. Parker & Jones, 1860*a*: 30, 37. No figure.

TYPE LOCALITY. Recent; Indian Ocean (no further details given).

REMARKS. There are no specimens so recorded, under any combination, in the Catalogue. A search of the Indian Ocean part of the collection, by a specialist, is needed to recognize this form.

Orbitolina concava Lamarck var. ***simplex*** Parker & Jones, 1860*a*

TYPE REFERENCE. Parker & Jones, 1860*a*: 29, 37. No figure

TYPE LOCALITY. Fossil; Tertiary from Grignon, France.

REMARKS. There are no specimens, under any combination of name, recorded in the Fossil Catalogue. Jones makes one reference to *Gypsina vesicularis* (p. 100, LXXXIV.3) P47612 from Grignon but this single specimen does not resemble the type description of var. *simplex* in any way. A Grignon record of *Patellina*? on p. 101, (LXXXIV.32) P47632, needs the attention of a specialist.

Orbitolina concava Lamarck var. ***sphaerulata*** Parker & Jones, 1860*a*

LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3599. Fiji.

TYPE REFERENCE. Parker & Jones, 1860*a*: 33, 38. No figure.

LOCALITIES. Recent; from Fiji and New Zealand (no further details given).

REMARKS. A unfigured lectotype (ZF3599) was designated, by Loeblich & Tappan (1964: C629) from Rewa reef, Fiji. One paralectotype exchanged with the U.S. National Museum of Natural History is figured by them (1964: fig. 501.1) but the remaining paralectotypes (ZF3598) are in the BM(NH). No specimens from New Zealand are named as such, but there are references to *Tinoporus baculatus* Mont-fort (pp. 242, 243, CXVI.7, 8) 1894:4:3:1800–1, which may be conspecific.

Orbitolina sphaerulata (*O. concava* var. *sphaerulata*) is the type species of *Baculogypsina* Sacco.

Orbitolina concava Lamarck var. ***sphaerulolineata*** Parker & Jones, 1860*a*

TYPE REFERENCE. Parker & Jones, 1860*a*: 34, 38. No figure.

TYPE LOCALITY. Fossil; uppermost Cretaceous from Ciply, Belgium.

REMARKS. Also referred to by Parker & Jones (1865: 438), from Fiji, under *Tinoporus sphaerulo-lineatus*. There are no Catalogue records of any material from Ciply or of this variety under any combination of the name.

Orbitolina concava Lamarck var. ***vesicularis*** Parker & Jones, 1860*a*

LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3600. From Jukes' dredging no. 2.

TYPE REFERENCE. Parker & Jones, 1860*a*: 31, 38. No figure.

TYPE LOCALITY. Recent; from Australia (no further details given).

REMARKS. Recorded as *Gypsina vesicularis* in the Recent Catalogue (pp. 124, 135, 139, 144). Loeblich & Tappan (1964: C694–8) designated a lectotype (ZF3600) from Jukes' dredging no. 2, 14 fathoms. Two notes in Jones' Recent Catalogue, on p. 233, gives this locality as '. . . probably from near south of Raine Islet', and in a footnote referring to CX.31, '. . . dredged up from the bottom at 14 fathoms, July 31st 1844, North of Sir C. Hardy's inside reefs on N.E. Coast of Australia . . . and this is most probably the locality and depth for all of CX slides. . . .' (i.e. Jukes' no. 2). Loeblich & Tappan's figured paralectotype (1964: fig. 567.1–2) possibly came from a suite of four specimens exchanged with the U.S. National Museum of Natural History (*ex* 1894:4:3:1737–8). Those specimens on (CX.22) 1894:4:3:1733 look more like *Gypsina globula*. Other paralectotypes have been remounted by Loeblich & Tappan from 1894:4:3:1738 and re-registered as ZF3601. Barker refers the present variety to *Gypsina* (1960: pl. 101, figs 9–12).

Planorbulina farcta (Fichtel & Moll) var. ***ungeriana*** (d'Orbigny) subvar. ***culter*** Parker & Jones, 1865

TYPE REFERENCE. Parker & Jones, 1865: 382, 421; pl. 19, fig. 1a, b.

TYPE LOCALITY. Recent; from 1080 fathoms, 2°20′N 28°44′W, tropical Atlantic Ocean.

REMARKS. Called *Planorbulina culter* in the Fossil Catalogue. There are no syntypes from north of the Island of St Paul, the type locality. From this locality (XXVIII) there are numerous specimens labelled *P. menardii*, but all are planktonic species and none agree with the figure of *culter*, nor are there any specimens identified by Jones under any combination in the Collection. Whittaker (1988: 135) discussed this taxon, under his description of *Osangularia bengalensis* (Schwager) from the Miocene of Ecuador, and concluded that although the name *culter* had been much used in the literature, its continued use cannot be defended and it would be better to regard it as a *nomen dubium*.

Planorbulina larvata Parker & Jones, 1865

Pl. 2, figs 4, 9

TYPE REFERENCE. Parker & Jones, 1865: 379, 380; pl. 19, fig. 3a, b.

TYPE LOCALITY. Recent, from 'the Indian Sea'.

REMARKS. The type locality is geographically very vague and the Catalogue makes no mention of *larvata*, so a lectotype is not designated since my identification of this species is subjective. There are numerous references to *P. mediterranensis* from the Indian Ocean which, in my opinion, are really *larvata*. The following records require comment. Of (XCIII.49–52) 1894:4:3:1377–80, only (XCIII.49) 1894:4:3:1377 (from the shells of *Chama hippopus*) contains specimens with the bilaterally symmetrical test and arrangement of the peripheral chambers, conforming to Cushman's (1927: 96) generic diagnosis of *Planorbulinella*, for which *larvata* is the type species. The remaining slides contain immature specimens, probably *mediterranensis*. From (XCIII.92–8) 1894:4:3:1421–7, only (XCIII.96) 1894:4:3:1425 contains forms, in my opinion, assignable to *larvata* (from the shells of *Chama gigas*), from which I have prepared three thin sections and figure one specimen (ZF4922). Loeblich & Tappan (1964: C694, 1988: 589) are in error in quoting the original citation as '*Planorbulina vulgaris* d'Orbigny var.*larvata* Parker & Jones, 1865'. Parker & Jones did in fact list a '*Planorbulina vulgaris* (var. *larvata*, nob.)' in 1860 (p. 294), but this is a *nomen nudum* because it does not satisfy the conditions of Article 12 of the ICZN (1985). Its elevation to species status and the inclusion of a figure by Parker & Jones (1865) validated the name.

Planorbulina retinaculata Parker & Jones, *in* Carpenter 1862

TYPE REFERENCE. Carpenter *et al*. 1862: 209.

TYPE FIGURE. Parker & Jones, 1865: pl. 19, fig. 2 (p. 380).

LOCALITIES. Recent; from the East and West Indies (no further information given).

REMARKS. This irregularly-developed species, a 'parasitic form' (Carpenter 1862: 209) on shells, has not been recorded under this name either in the Recent Catalogue, or in the Carpenter Collection at the Royal Albert Memorial Museum, Exeter (Murray & Taplin's (1983) unpublished Catalogue), and the exotic figured specimen has not been found. Parker does have some wildly growing specimens of *Planorbulina mediterranensis* in his Collection, on (XCIII.95) 1894:4:3:1424, (XCIII.96) 1894:4:3:1425 and (XCIII.97) 1894:4:3:1426. These were removed from the shells of *Chama gigas*, in the Indian Ocean, and they might be small, poorly developed variants of the impressive figured specimen.

Planularia pauperata Jones & Parker, 1860*a*

Fig. 2.3, 4

TYPE REFERENCE. Jones & Parker, 1860*a*: 454; pl. 20, fig. 39.

TYPE LOCALITY. Fossil; 'probably Upper Triassic from a blue clay, Chellaston, three miles south of Derby, England' (*sic*; see note below and p. 56).

REMARKS. This is '. . . indicated as a variety not previously recognised' (see top of p. 454), but of what, the authors do not make absolutely clear. The material from which this specimen was recovered was brought to Messrs Cubitt's works from Chellaston (p. 452). However, in the Fossil Catalogue (p. 4), it is clearly stated that although the Red Clay came from Chellaston, the Blue Clay, (VIII.1–8) P44813–9 and P44635–6, is probably some Lias brought by the same conveyance (canal barge?), possibly from Leicestershire. In the Catalogue, beside each species, is a figure number referring to the paper used by Jones to identify it, but pl. 20, fig. 39 is not given against any specimen, even under a genus with the same specific name (e.g. *Dentalina pauperata*). A careful re-examination of these slides, however, has revealed on VIII.1 (P44813) one specimen (P52792, here figured) which in my opinion is almost identical to the original figure. However since this specimen was not named *Planularia pauperata* by Jones a lectotype is not designated.

Polymorphina elegantissima Parker & Jones, *in* Brady, Parker & Jones 1870

Pl. 2, figs 7, 8; Fig. 1.3

LECTOTYPE (here designated). From Storm Bay, Tasmania (*ex* 1955:10:3:8–10), 1955:10:3:8.

TYPE REFERENCE. Brady, Parker & Jones, 1870: 231; pl. 40, fig. 15a–c.

LOCALITIES. Recent; from shell sand near Melbourne, Australia, and soundings in Storm Bay, Tasmania.

REMARKS. The only locality given for this species in the Catalogue (p. 223, (CIII.59) 1894:4:3:1580) is Melbourne shore sand. However, the smaller of the two specimens originally illustrated (pl. 40, fig. 15b, c) is from Storm Bay, Tasmania, a locality not recorded in the Catalogue. However, in the H.B.Brady Collection at the BM(NH) there are four specimens (1955:10:3:7, 1 specimen and 1955:10:3:8–10, 3 specimens) from Storm Bay, given to Brady from A. Roberts material, which are all syntypes since the type description was in a joint publication; it is from the latter that the lectotype is chosen. This is an instance where a species name is attributed by Brady *et al.* to specimens earlier found and named by Parker & Jones.

Brady (1884) records the species as being best known from the Australian region. Cushman & Ozawa (1929: 76) refer the species to *Sigmoidella.* In 1930, the same authors, considering that the larger specimen illustrated by Brady *et al.* (1870: pl.15a) was not an *elegantissima*, renamed it *Sigmoidella kagaensis*.

Polymorphina frondiformis Wood, *in* Jones, Parker & Brady, 1866

Pl. 2, figs 13, 14

LECTOTYPE (here designated). From Sutton, England (*ex* P48326), P52788.

TYPE REFERENCES. Jones, Parker & Brady, 1866: Appendix 1–2 footnotes; pl. 1, figs 62, 63, 69; pl. 4, figs 11–14. See also Jones *et al.* 1896 (part 3 of the Crag Monograph): 271 for the first description.

TYPE LOCALITY. Fossil; 'Older Pliocene, Lower (White, Polyzoan or Suffolk) Crag' from Sutton, Suffolk, England.

REMARKS. The Fossil Catalogue (p. 158, CXXX.38–42) P48324–7, lists many specimens from the Searles V. Wood collection. Additional S.V. Wood material from the Coralline Crag of Gedgrave, Orford (Suffolk, England) and Sutton are present in the micropalaeontology collection at the BM(NH). Here, the specific name *frondiformis* is attributed to Wood *in* Jones, Parker & Brady, since the name given to the fossil by Wood (*in* Morris 1843: 62), was originally a *nomen nudum* (Article 12, ICZN 1985: 33), he having neither described or figured it.

Polymorphina hirsuta Brady, Parker & Jones, 1870

TYPE REFERENCE. Brady, Parker & Jones, 1870: 243; pl. 42, fig. 37.

TYPE LOCALITIES. Fossil; from the 'Pliocene Crag of Sutton near Colchester' (*sic*), England. Recent of the West Indies.

REMARKS. There are no named fossil or Recent specimens in the collection, but, on a fossil slide, (CXXX.38) P48324, from Sutton, there is one 'finely gibbous' poorly preserved specimen which requires further study.

Cushman & Ozawa (1930: 69) consider this species should be included within *Globulina gibba* var. *punctata* d'Orbigny.

Polymorphina regina Brady, Parker & Jones, 1870

Pl. 2, figs 15, 16

LECTOTYPE (here designated). From Storm Bay, Tasmania (*ex* 1955:10:3:14–16) 1955:10:3:14.

TYPE REFERENCE. Brady, Parker & Jones, 1870: 241; pl. 41, fig. 32a, b.

TYPE LOCALITY. Recent soundings from Storm Bay, Tasmania.

REMARKS. There are no specimens listed in the Recent Catalogue. However, in the H.B. Brady Collection there is a slide (1955:10:3:14–16), marked *Polymorphina regina,* from Storm Bay (A. Roberts material). This is syntypic, as on the reverse it is labelled in pencil 'N. sp.' and the type description was in a joint publication. The lectotype I have chosen from this slide is possibly the figured specimen which was originally illustrated by a reversed image.

P. regina was placed in *Guttulina* by Cushman & Ozawa (1930: 34).

Polymorphina variata Jones, Parker & Brady, 1866

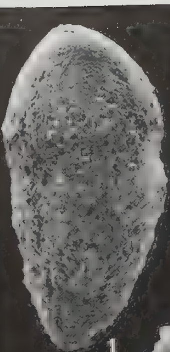
Pl. 2, figs 10–12

LECTOTYPE (here designated). From Sutton (*ex* P48319) P52790.

TYPE REFERENCE. Jones, Parker & Brady, 1866: Appendix 1–2 footnotes; pl. 1, figs 67, 68.

TYPE LOCALITY. Fossil; 'Older Pliocene, Lower (White, Polyzoan or Suffolk) Crag' (= Coralline Crag), Sutton, Suffolk, England.

REMARKS. Recorded in the Catalogue (CXXX.28–30) P48317–19. The figured specimens have not been recognized with certainty, but a syntype (Pl. 2, figs 10, 11) has been selected as lectotype. But another specimen (Pl. 2, fig. 12)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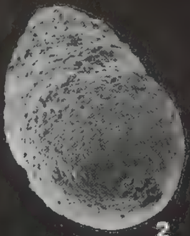
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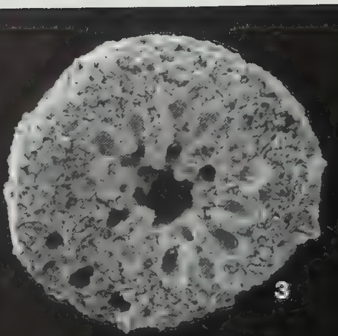
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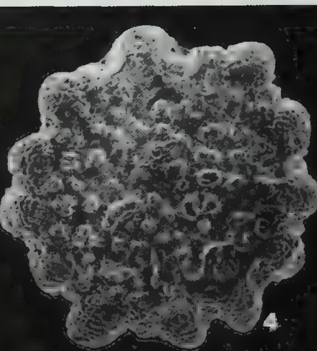
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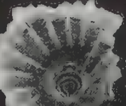
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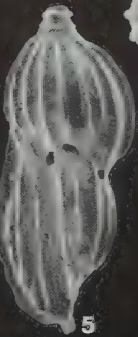
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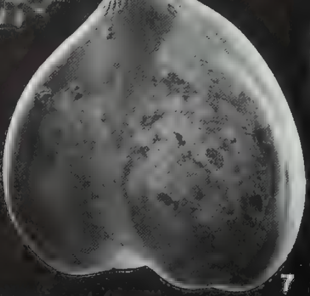
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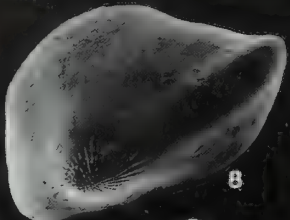
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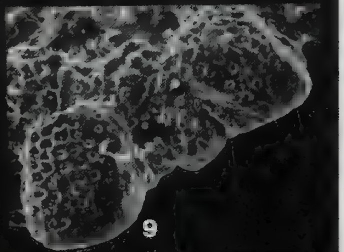
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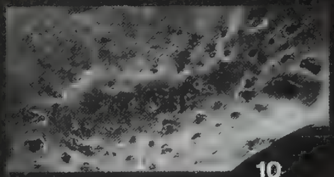
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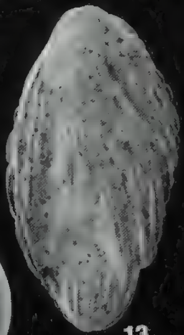
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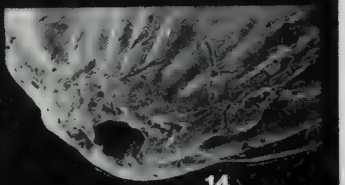
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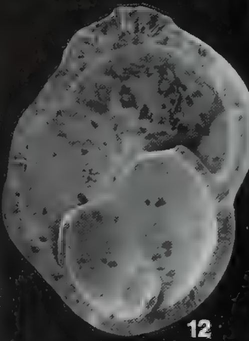
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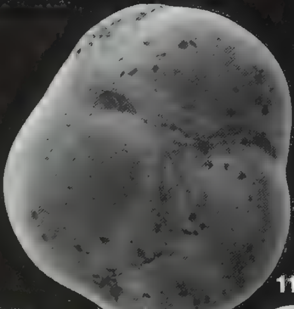
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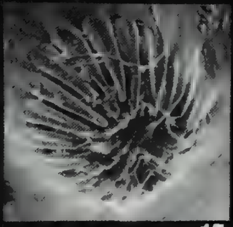
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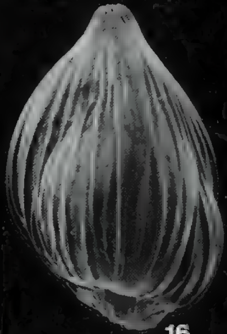
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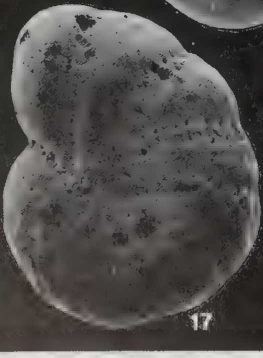
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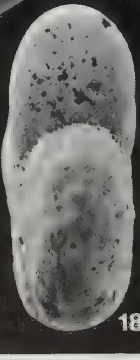
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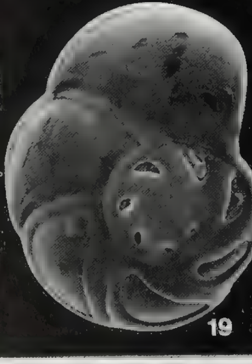
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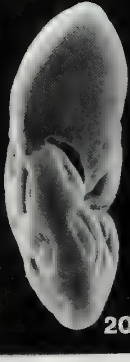
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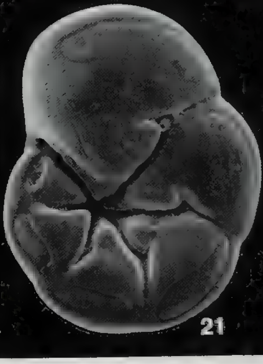
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differs from the type figure (1886: pl. 1, fig. 67) only in the position of the initial chamber. Slide CXXX.30 (P48319) contains an individual indicated to have been figured by Jones *et al.* (1896: 272; pl. 5, fig. 27).

The species is placed in *Pseudopolymorphina* by Cushman & Ozawa (1930: 101).

Polystomella arctica Parker & Jones, *in* Brady, 1864

Pl. 2, figs 17, 18

LECTOTYPE (here designated). From the Shetland Islands (*ex* 1964:2:12:274–317), 1964:2:12:287.

TYPE REFERENCE. Brady, 1864: 471; pl. 48, fig. 18.

TYPE LOCALITY. Recent; between 75–90 fathoms, Shetland Islands.

REMARKS. There are no syntypes in the Parker Collection. Said, in the original description, to be '. . . mostly dark-coloured, generally brown. . .', specimens from the type locality in the H.B. Brady Collection (syntypes, as the species was described in a joint publication) are generally colourless; one of these has been selected lectotype. The authorship was cited by Brady 1864 as 'Parker and Jones MS' but in the plate explanation the 'MS' is omitted; authorship is probably best attributed to Parker & Jones, *in* Brady, 1864 (see earlier explanation p. 48). One specimen from Hunde Island, 28–30 fathoms, has been separated from slide (XXV.2K) 1894:4:3:183 by Loeblich & Tappan and re-registered as ZF2674, in preparation for designation as a neotype, but to my knowledge this was never formalized.

P. arctica is the type species of *Elphidiella* Cushman.

Pullenia obliquiloculata Parker & Jones, 1865

NEOTYPE. The so-called 'lectotype' selected by Bolli, Loeblich & Tappan 1957, ZF3583. (See below and p. 48). From the Abrolhos Bank.

TYPE REFERENCE. Parker & Jones, 1865: 365, 368; pl. 19, fig. 4a, b.

LOCALITIES. Recent; from the Abrolhos Bank at 260 fathoms off Brazil, 22°54′S 40°37′W; also from the tropical Atlantic at 1080 fathoms, 2°20′N 28°44′W, and from the Indian Ocean at 2200 fathoms, 5°37′S 61°33′E.

REMARKS. A 'lectotype' (ZF3583) was designated by Bolli, Loeblich & Tappan (1957: 33) (*ex* slide 1894:4:3:1045) from the Abrolhos Bank. No specimen of this name is recorded in Jones' Catalogue from this locality but he does list *Pullenia sphaeroides* and *P. quinqueloba*. Loeblich & Tappan must have searched all slides from the type localities and located a specimen which, in their opinion, Jones had not correctly identified, but as there is no evidence this was a syntype the selection is tantamount to neotype designation, as I here regard it. There is a record of a *Pullenia sphaeroides* from the tropical Atlantic, 1080 fathoms, in the Catalogue (p. 63, XXVIII.'8', slides 10–12) 1894:4:3:370–372. *Pullenia obliquiloculata,* itself, is recorded in the Catalogue on p. 201, (XCI.182) 1894:4:3:1313 from the Indian Ocean, Tropical (= No 9 of Captain Pullen's list, 5°37′S 61°33′E, 2200 fathoms), but Banner & Blow (1967: 128) consider this to be incorrectly identified.

The species is the type of *Pulleniatina* Cushman. The generic diagnosis has been emended and the 'lectotype' refigured by Banner & Blow (1967: 137; pl. 3, fig. 4a–c).

Pulvinulina concentrica Parker & Jones, *in* Brady, 1864

Pl. 2, figs 19–21

LECTOTYPE (here designated). From 75–90 fathoms, Shetland Islands (*ex* 1959:5:11:138–141), 1959:5:11:138.

TYPE REFERENCE. Brady, 1864: 470; pl. 48, fig. 14.

LOCALITIES. Recent; at 75–90 fathoms, Shetland Islands; also from the Mediterranean Sea and the Bay of Biscay, France.

REMARKS. In H.B. Brady's Collection in the BM(NH) there are named specimens of *concentrica* from the Shetland Islands, at 75–90 fathoms (1959:5:11:138–141). One specimen is now an unrecognizable fragment, the second is little better, the third mounted in apertural view is in a very fragile state

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PLATE 2

Figs 1–3 *Lituola nautiloidea* Lamarck var. *soldanii* Jones & Parker. Figs 1, 2, Lectotype P52787, here designated; Miocene of San Domingo. Side and oblique-apertural view, respectively, × 40. Fig. 3, Paralectotype P52787a, same locality; test fractured across to show internal partitions, × 60.

Figs 4, 9 *Planorbulina larvata* Parker & Jones. ZF4922, Indian Ocean. Fig. 4, ventral view, × 35; Fig. 9, oblique-peripheral view showing apertures, × 80.

Figs 5, 6 *Nodosaria* (*Marginulina*) *raphanus* (Linnaeus) var. *falx* Jones & Parker. ZF4921, near Crete. Side and apertural views, respectively, × 75.

Figs 7, 8 *Polymorphina elegantissima* Parker & Jones. Lectotype 1955:10:3:8, here designated; Storm Bay, Tasmania. Side and oblique-apertural views, respectively, × 45. See also Fig. 1.3 (p. 56).

Figs 10–12 *Polymorphina variata* Jones, Parker & Brady. Figs 10, 11, Lectotype P52790, here designated; Coralline Crag, Sutton, Suffolk. Detail of aperture (× 50) and side view (× 20), respectively. Fig. 12, Paralectotype P52789, same locality; internal view of broken specimen, × 25.

Figs 13, 14 *Polymorphina frondiformis* Wood, *in* Jones, Parker & Brady. Lectotype P52788, here designated; Coralline Crag, Sutton, Suffolk. Fig. 13, side view, × 10; Fig. 14, oblique view showing aperture detail , × 50.

Figs 15, 16 *Polymorphina regina* Brady, Parker & Jones. Lectotype 1955:10:3:14, here designated; Storm Bay, Tasmania. Fig. 15, oblique view showing detail of aperture, × 175; Fig. 16, side view, × 50.

Figs 17, 18 *Polystomella arctica* Parker & Jones, *in* Brady. Lectotype 1964:2:12:287, here designated; Shetland Is. Side and apertural views, respectively, × 40.

Figs 19–21 *Pulvinulina concentrica* Parker & Jones, *in* Brady. 1964:2:12:545, from dredged material from the Shetlands. Dorsal, edge and ventral views, respectively, × 46.

All scanning electron photomicrographs.

and the fourth is clearly that figured in the Challenger Report (Brady 1884: pl. 105, figs 1a–c), but is not the specimen originally figured in 1864. The Challenger Expedition never went to the Shetlands so it is probable that the specimen figured by Brady in 1884 is a syntype, particularly since on the slide Brady has written 'Figured Shetland paper, also CV.1'. Although no mention is made in the Challenger text (1884: 686) that this original specimen had been lost, it could be argued that Brady did not reproduce it because it no longer existed. This specimen (1884: pl. 105, fig. 1a–c) is here designated lectotype (1959:5:11:138), but not refigured. Fortunately there are other specimens from dredged material in the Shetlands (1964:2:12:545–9) which are in almost perfect condition (Pl. 2, figs 19–21) and illustrate the characters of the species better than the lectotype. The apertural view of the lectotype was not shown at the time of the original description but my figured specimen (Pl. 2, fig. 20; 1964:2:12:545) has an identical aperture, of the *Stomatorbina* type, confined to the ventral (umbilical) side (see Uchio 1952; also Loeblich & Tappan 1988: 554, pl. 600, figs 7–15).

Pulvinulina concentrica is not recorded in Jones' Catalogue; however, since in the original citation this species is considered to be 'a variety of *P. repanda* F. & M., sp.', the reports of the latter species and its varieties from the beach at Leghorn (XXXVI.8) 1894:4:3:447, from on a sand bank at nearly highwater mark, The Lido, Venice (XXXIX.5) 1894:4:3:489, and from the shore sand of Crete (LVI.19) 1894:4:3:735 (this in my opinion does not contain *concentrica*), which are all in the 'Mediterranean Sea', must be mentioned. No specimens have been located from the Bay of Biscay (50 miles SW of Ushant, in 70 fathoms, is the only locality mentioned in the Catalogue, (XIII.9, 11–14) 1894:4:3:397, 399–402, and it does not contain this species). See also p. 48.

Pulvinulina repanda Fichtel & Moll var. *menardii* d'Orbigny subvar. *pauperata* Parker & Jones, 1865

LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3574. From the Celtic abyssal.

TYPE REFERENCE. Parker & Jones, 1865: 395; pl. 16, figs 50, 51.

LOCALITIES. Recent; from 1450–2350 fathoms, between 52°25′ and 48° north latitude, North Atlantic Ocean, and from 'Boreal' tract towards Newfoundland Bank, 50°6′N 48°45′W, North Atlantic Ocean; also from the 'Celtic' tract, 52°16′30″N 29°28′30″W, North Atlantic Ocean; from 1080 fathoms, 2°20′N 28°44′W in the tropical Atlantic; and from 900 and 1120 fathoms, 36°58′S 51°49′E, Indian Ocean.

REMARKS. In the Recent Catalogue it is recorded as *Pulvinulina pauperata*. There is a record from the Celtic abyssal, 52°16′30″N 29°28′30″W at 2176 fathoms (XXVII.85(1)) 1894:4:3:319, and this specimen was remounted and designated lectotype (ZF3574) by Loeblich & Tappan (1964: C582), but remains unfigured. There is one specimen from the Boreal abyssal (XXVII.80(1)) 1894:4:3:309. I can find no specimen corresponding to the record listed on p. 62 of the Catalogue (XXVIII.'8', 2) 1894:4:3:362, from the tropical Atlantic, 2°20′N 28°44′W, at 1080 fathoms, north of the Island of St Paul, a sounding made by Captain Pullen on HMS Cyclops in 1858 and given to Parker by Mr A. Hilton.

This taxon is the type species of *Laticarinina* Galloway & Wissler, a genus re-studied by Cushman & Todd (1941, 1942). Loeblich & Tappan (1988) consider *Laticarinina* to be a senior synonym of *Parvicarinina* Finlay, and (1988: 579) provide additional information on the umbilical openings and subequatorial apertures of this genus. Whittaker (1988: 129) reviews evidence that *P. pauperata* cannot be a junior synonym of *Robulina halophora* Stache.

Pulvinulina sacculata Parker & Jones, 1876

TYPE REFERENCE. Jones & Parker, 1876: 284; text-figs 1–3.

TYPE LOCALITY. Recent; from the English Channel at 70 fathoms, 50 miles southwest of Ushant Island (Isle d'Ouessant), Department of Finistère, France.

REMARKS. It is possible that Jones, when he came to compile the Catalogue on the Ushant material nearly 20 years after, could, in the light of subsequent experience, recognize only the more common species of *Pulvinulina*, viz. *P. auricula*, *menardii* (and varieties *pulchella, punctulata*) and *repanda* (and varieties) on (XXX.2, 9, 11–15) 1894:4:3:390, 397, 399–403. Identification was certainly not aided by the rather poor original illustration of *sacculata*. From my examination of the material I conclude that XXX.2 and 9 do not contain this species; the other slides (XXX.11–15) require specialist examination.

Rotalia beccarii (Linnaeus) var. *annectens* Parker & Jones, 1865

Pl. 3, figs 1–3

LECTOTYPE (here designated). From Hong Kong (*ex* 1894:4:3:1468), ZF4923.

TYPE REFERENCE. Parker & Jones, 1865: 387, 422; pl. 19, fig. 11a–c.

TYPE LOCALITIES. Recent; from anchor mud, 8 or 9 fathoms, Hong Kong, China; also coral reef, Fiji Islands, South Pacific.

REMARKS. Recorded in the Catalogue as *Rotalia annectens*. There are syntypes from Hong Kong anchor mud, 8 or 9 fathoms, China Sea: (XCVI.2) 1894:4:3:1461 contains very small specimens which could be equated with those found by Millett (1904: 505) in the Malay Archipelago; (XCVI.9) 1894:4:3:1468 contains several adult specimens, one of which is selected lectotype. No examples have been found from the Fiji Islands.

This is the type species of *Cavarotalia* Müller-Merz, a genus which Loeblich & Tappan (1988: 667) subsequently placed into synonymy with *Rotalidium* Asano.

Rotalia beccarii (Linnaeus) var. *craticulata* Parker & Jones, 1865

Pl. 3, figs 7–9

TYPE REFERENCE. Parker & Jones, 1865: 387, 388 and 422; pl. 19, fig. 12a–c.

TYPE LOCALITY. Recent, from coral reef and adherent to a hydroid polyp, Fiji Islands, South Pacific Ocean.

REMARKS. There are no specimens so named in the Catalogue, but there are several I have found under the name of *Polystomella crispa* (Linné) (which, at the quick glance that was all Jones probably gave to them, is superficially similar) on (XCVII.11) 1894:4:3:1823 from the Rewa reef of Viti Levu, Fiji and I have illustrated one specimen (ZF4926) from (CXVIII.3) 1894:4:3:1827, Fiji Islands (unlocalized). Since my identifications are subjective no lectotype has been chosen.

There is a record in the Fossil Catalogue of '*Rotalia*, sp. near *Rotalia craticulata*, P. & J. & *R. calcar*, d'O.' from the Chalk of Gravesend, Kent (XLV.24) P46711, but this is clearly a misidentification. Its correct generic placement within the Elphidiidae is uncertain.

Rotalia beccarii (Linnaeus) var. *dentata* Parker & Jones, 1865

Pl. 3, figs 4–6

LECTOTYPE (here designated). From Bombay harbour (*ex* 1894:4:3:1438), ZF4925.

TYPE REFERENCE. Parker & Jones, 1865: 387–8 and 422; pl. 19, fig. 13a–c.

TYPE LOCALITY. Recent; from anchor mud, Bombay Harbour, India.

REMARKS. Syntypes are recorded in the Catalogue (p. 209), as *Rotalia dentata,* from the 'Arabian Sea, Bombay Harbour anchor mud', (XCIV.3–4, 9–11) 1894:4:3:1438–9, 1444–46, accompanied by typical *beccarii*; a lectotype is formally erected from the first of these slides. There is a further record (p. 161) from 30 fathoms in the Gulf of Suez, = No. 6 of Pullen's MS list, 28°38'N 33°9'E, Gulf of Suez (LXXXIX.34) 1894:4:3:1116.

The species is placed in *Asterorotalia* by Billman *et al.* (1980: 96).

Rotalia schroeteriana Parker & Jones, *in* Carpenter 1862

Figs 1.4, 3.1–3

LECTOTYPE (here designated). From slide 263/1903-634, W.B. Carpenter collection in Royal Albert Memorial Museum, Exeter, England; it is the large, centrally placed, possibly microspheric specimen.

TYPE REFERENCE. Carpenter *et al.* 1862: 213; pl. 13, figs 7–9.

TYPE LOCALITY. Recent; Philippines.

REMARKS. In the W.B. Carpenter Collection in Exeter, listed under numbers 634–636 in Murray & Taplin's Catalogue, are specimens named '*Rotalia schrötteriana (Faujasina)*' from the Philippines. These specimens can be considered syntypes and from one of the slides (634) a lectotype has been chosen. Slides 635 and 636 contain thin sections in Canada balsam mounts, but none of these correspond to those figured by Carpenter. A thin-sectioned specimen in the Williamson Collection in the BM(NH), labelled *Faujasina* sp. (Parker & Jones synonymized Williamson's specimens of this name), matches none figured by Williamson (1853), or Parker & Jones (*in* Carpenter, 1862) (see Whittaker & Hodgkinson, 1979: 78). In Jones' Catalogue, the only record (p. 160–1) is from the Gulf of Suez, which cannot be regarded as truly 'tropical' as it lies north of the Tropic of Cancer.

R. schroeteriana is the type species of *Pseudorotalia* Reiss & Merling. Unfortunately, Billman *et al.* (1980) include the type species of *Asanoina* Finlay in *Pseudorotalia*, which automatically gives the former priority, but nevertheless still continue to use *Pseudorotalia*. Loeblich & Tappan (1988: 666–7), in their 'Remarks' on *Pseudorotalia*, consider the two genera to be distinct.

Sphaeroidina bulloides d'Orbigny var. *dehiscens* Parker & Jones, 1865

LECTOTYPE. Designated by Bolli, Loeblich & Tappan 1957, ZF3580. From north of St Paul's Island.

TYPE REFERENCE. Parker & Jones, 1865: 369; pl. 19, fig. 5.

LOCALITIES. Recent; from 1080 fathoms, 2°20'N 28°44'W (north of the Island of St Paul, a sounding made by Captain Pullen on HMS Cyclops in 1858), in the tropical Atlantic Ocean; and from 2200 fathoms, 5°37'S 61°33'E, in the Indian Ocean.

REMARKS. It is recorded in the Catalogue (pp. 63 & 194) as *Sphaeroidina dehiscens*. Paralectotypes have been located on XXVIII.'8'.8 (1894:4:3:368), the same slide from which Bolli, Loeblich & Tappan (1957) designated a lectotype (ZF3580). A record from the Gulf of Aden, (XC.145) 1894:4:3:1275, the only one from the Indian Ocean, is incorrect, nothing conspecific with the lectotype being present.

It is the type species of *Sphaeroidinella* Cushman.

Textularia agglutinans d'Orbigny var. *biformis* Parker & Jones, 1865

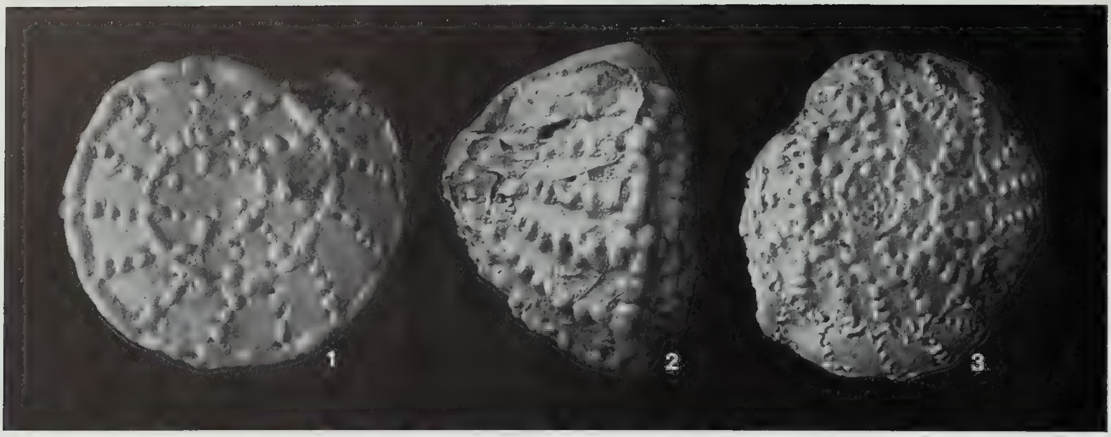
LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3639. From Hunde Islands, 60–70 fathoms.

TYPE REFERENCE. Parker & Jones, 1865: 370; pl. 15, figs 23a, b, 24.

LOCALITIES. Fossil; in the Gault and the Chalk of England. Recent; in 60–70 fathoms off Hunde Islands in South-east, or Disco Bay, Davis Straits, west coast of Greenland, 68°50'W, 53°N.

REMARKS. Nothing under this name is recorded in the Fossil Catalogue, but there are records of *T. agglutinans* and varieties on (XL.26–7, 35–9) P46121–2, P46130–4; (XLII.2) P46580; (XLIII.4) P46634; (XLIV.3) P46672 and (XLV.6–7) P46692–3; all from the Chalk: they need further investigation by a specialist. From the Recent, it is recorded in the Catalogue (p. 35) as *Textularia biformis* (which Jones considered should be called *Spiroplecta*), from Hunde Islands No. 5 between 60–70 fathoms (XXV.5,4 and 5,5) 1894:4:3:194, 1894:4:3:195. Some of these specimens have been remounted by Loeblich & Tappan and a lectotype has been designated but not figured (1964: C251); ZF3639 (*ex* 1894:4:3:195). Paralectotypes are re-registered ZF3637 (*ex* 1894:4:3:194). There is a further record from Hunde Islands No. 4, 50–70 fathoms (XXV.4A) 1894:4:3:187; here the specimens have been remounted (ZF3638) and wrongly labelled paralectotypes.

As an aside, the statement on the type depository in the Ellis & Messina Catalogue (1940 *et seqq.*) possibly refers to the soundings, collected by Mr Sutherland, which were deposited in the Museum of Practical Geology, Jermyn Street, London, and lent to Parker & Jones for study and presumably returned. This material, later housed at the Geological Museum in South Kensington, London, is now at



Figs 3.1–3 *Rotalia schroeteriana* Parker & Jones. All from the Carpenter Collection, in the Royal Albert Museum, Exeter; register number 263/1903-634. Philippines. Fig. 1, Paralectotype (position 6 on slide), probable megalospheric form, dorsal view, × 35. Fig. 2, Paralectotype (position 13 on slide), edge view showing intercameral aperture, × 35. Fig. 3, Lectotype, here designated (position 11 on slide), probable microspheric form, dorsal view, × 20.
Micrographs taken of uncoated specimens in environmental chamber, attached to ISI (ABT) 55 scanning electron microscope.

the British Geological Survey Headquarters at Keyworth. However, Dr I. Wilkinson of the British Geological Survey (personal communication) tells me that *biformis* was among much foreign material transferred to the British Museum (Natural History) in 1880. Since the above slides were clearly made by Parker, they must either not have been presented at his death but were incorporated by Jones into the collection at the time of cataloguing, or they were not among the specimens presented in 1880.

This taxon is the type species of *Spiroplectammina* Cushman.

Textularia annectens Parker & Jones, 1863

LECTOTYPE. Designated by Loeblich & Tappan 1964, P41668. From the Gault of Biggleswade (England).

TYPE REFERENCE. Parker & Jones, 1863: 92, 96, text-fig. 1 (p. 92).

LOCALITIES. Fossil; from the Lower Cretaceous, Gault at Biggleswade, Bedfordshire, England; and from other unlocalized Jurassic, Oolite clays.

REMARKS. Syntypes are listed in the Fossil Catalogue (p. 30) as *Spiroplecta annectens* (XXXIV.7–10). A lectotype (P41668) was designated by Loeblich & Tappan (1964: C272), but not figured. It and the paralectotypes (P41667) were removed from XXXIV.7–10 by them and remounted. The species is also recorded in the Fossil Catalogue on p. 23, from the Gault at Kentish Town, London (XXX.2) and on p. 25 from Leacon Hill, Charing, Kent (XXXI.11). In the Recent Catalogue it is listed under *Textularia annectens*.

It is the type species of *Spiroplectinata* Cushman.

Textularia agglutinans d'Orbigny var. *folium* Parker & Jones, 1865

LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3595. From shore sand, Melbourne.

TYPE REFERENCE. Parker & Jones, 1865: 370, 420; pl. 18, fig. 19.

TYPE LOCALITY. Recent; from shore sand near Melbourne, Australia.

REMARKS. Recorded in the Recent Catalogue as *Textularia folium* on pp. 100 (Mediterranean), 194 (Gulf of Aden) and 219 (Melbourne shore sand). It is from among the last-named syntypes, CII.2 (1894:4:3:1521), that a lectotype (ZF3595) was selected but not figured by Loeblich & Tappan (1964: C526–8); the Melbourne paralectotypes were remounted and re-registered as ZF3594. These specimens are mentioned by Hayward & Brazier (1980: 108), with a paralectotype figured in their pl. 3, figs 1, 2, and again by Hayward (1990: 48; pl. 4, figs 6, 7).

It is the type species of *Bolivinella* Cushman.

Textularia barrettii Parker & Jones, 1876*a*

LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3635. From Jamaica.

TYPE REFERENCE. Jones & Parker, 1876*a*: 99, text-figs.

LOCALITIES. Fossil; Pliocene (?) from unspecified localities. Recent; from 'Dragage (dredging) No 3, de 100 à 250 brasses (fathoms) (182–457m) environs de Jamaïque', British West Indies.

REMARKS. Incorrectly recorded in the Fossil Catalogue (p. 129) as *Terebratula barrettii* (CXI.16–20) P48103–7, from the Miocene of San Domingo, and correctly from the Miocene Pteropod Marl of Jamaica, collected by Lucas Barrett, (CXII.1 and 9) P48149 and P48157. There are no records from Pliocene deposits. In the Recent Catalogue the locality is given only as Jamaica, 100–250 fathoms (Lucas Barrett, 1862). (LXXX.17) 1894:4:3:973 contains one specimen. Of those originally mounted in (LXXX.15–6) 1894:4:3:971–2, one (ZF3635) has been designated lectotype, but not figured, by Loeblich & Tappan (1964: C299–300) and the remaining paralectotypes have been remounted and re-registered as ZF3636.

It is the type species of *Textulariella* Cushman.

Textularia (Bigenerina) tubulifera Parker & Jones, 1863

NEOTYPE. The so called 'lectotype' selected by Gibson *et al.* 1991, P52571. (See below and p. 48). From Grignon.

TYPE REFERENCE. Parker & Jones, 1863: 94, text-fig. 2.

TYPE LOCALITY. Fossil; Eocene from Grignon, France.

REMARKS. Not recorded either under *Textularia* or *Bigenerina* in the Fossil Catalogue. However, under the unlikely heading of *Textularia* sp., individuals of this species, from the Calcaire Grossier of Grignon, have been recognized by Dr T.G. Gibson of the United States Geological Survey. He has selected a 'lectotype', P52571 (*ex* LXXXIV.53), which should strictly be a neotype since his identification is subjective, and 'paralectotypes' P42572–5 (*ex* LXXXIV.52). Moreover, from LXXXIV.53 (P47653), as well as *tubulifera,* he has described a new species *Tubulogenerina nodosa* Gibson (*in* Gibson *et al.*, 1991: 311).

T. tubulifera is the type species of *Tubulogenerina* Cushman.

Triloculina striatotrigonula Parr, 1941

TYPE REFERENCE. Parr, 1941: 305.

TYPE FIGURE. Brady, 1884: pl. 4, fig. 10 a, b (*non* fig. 8).

TYPE LOCALITY. Recent; from Challenger station 162, off East Moncoeur Island, Bass Strait, Australia in 38–40 fathoms.

REMARKS. Originally a *nomen nudum*, as it was merely listed by Parker & Jones (1865: 438) in their Table 10, as *Triloculina striatotrigonula,* nov., and not figured. Brady (1884) described and figured a new species *Miliolina insignis*, which was considered by Parr (1941) to embrace more than one species. He therefore re-introduced Parker & Jones' name *striatotrigonula* for those specimens illustrated by Brady (1884: pl. 4, fig. 10a, b), which were, in his opinion, not *insignis* and which, coming from Australia, were sufficiently distinct to avoid any confusion with other species. In doing so, Parr validated the name, not under Parker & Jones' authorship, as he claimed, but under his own (see Ellis & Messina 1940 *et seqq*.). The specimen illustrated by Brady (1884: pl. 4, fig. 10b), ZF1869, is not the same specimen as his fig. 10a (ZF1868), but the two are, in my opinion, conspecific. Parr was unaware that two specimens were involved in the illustrations.

Trochammina (Webbina) hemisphaerica Jones, Parker & Brady, 1866

'HOLOTYPE'. Isolated by Loeblich & Tappan, 1964, P41659. From the Crag of Sutton, Suffolk, England.

TYPE REFERENCE. Jones, Parker & Brady, 1866: 27; pl. 4, fig. 5.

TYPE LOCALITY. Fossil, Crag from Sutton (Mr Wood's collection) (=Coralline Crag).

REMARKS. Also referred to in the Fossil Catalogue as *Webbina hemisphaerica* (p. 159) and in the type reference (p. 27) as *Trochammina (Webbina) irregularis* var. *hemisphaerica*. In the original description only one specimen is mentioned and this automatically becomes the holotype. However the piece of shell to which this specimen is attached, as drawn by Jones *et al.*, differs from the specimen restudied and illustrated by Loeblich & Tappan (1964: C535, fig. 420.7), P41659. For this reason the word 'holotype' appears in quotes above; this specimen isolated by Loeblich & Tappan is labelled 'Lower Crag, Sutton, Suffolk'. Jones gives its locality (Fossil Catalogue p. 159) as 'Lower Pliocene, (Crag); Suffolk: continued. Crag with *Cardita senilis*. Coll. S.V. Wood. Especially at Gedgrave.' The entry in the Catalogue records this specimen from CXXX.66, but a pencilled entry indicates that it was remounted from CXXX.64. I must assume that Jones was in error when compiling the Catalogue, although the locality details are unchanged.

This species is the type species of *Webbinella* Rhumbler, subsequently designated by Cushman, 1918.

Trochammina irregularis (d'Orbigny) var. *alternans* Jones & Parker, 1860

TYPE REFERENCE. Jones & Parker, 1860: 304. No figure.

TYPE LOCALITY. Given in the Ellis & Messina Catalogue (1940 *et seqq.*) as: Recent, in 300 fathoms off Crete, Mediterranean Sea. (I am unable to find this depth information in the type reference since the variety is not mentioned in the Table, but I suspect that the depth may be 360 fathoms; see below).

REMARKS. This generic name is not mentioned in the Catalogue either in its original form or abbreviated. There are no slides from the depth given in the Ellis & Messina Catalogue (1940 *et seqq.*), for the type locality. However from a depth of 360 fathoms, which may be meant, the species *Webbina clavata* and varieties are recorded on (LVII.1–4) 1894:4:3:748–51; this is mentioned here since Jones & Parker also regarded *clavata* as a variety of *T. irregularis*. There is a record of *Webbina irregularis alternans* by Jones *et al.* in part I of the Crag monograph (1866: 25). In the absence of a type figure, Jones, 30 years on, was probably unable to distinguish particular varieties. Now that *clavata* has been properly diagnosed (see below), a specialist in this group may wish to make *alternans* a *nomen dubium*, which alternative is important since Jones & Parker's name is a senior homonym of *Trochammina alternans* Earland, 1934 (the type species of *Alterammina* Brönnimann & Whittaker, 1988).

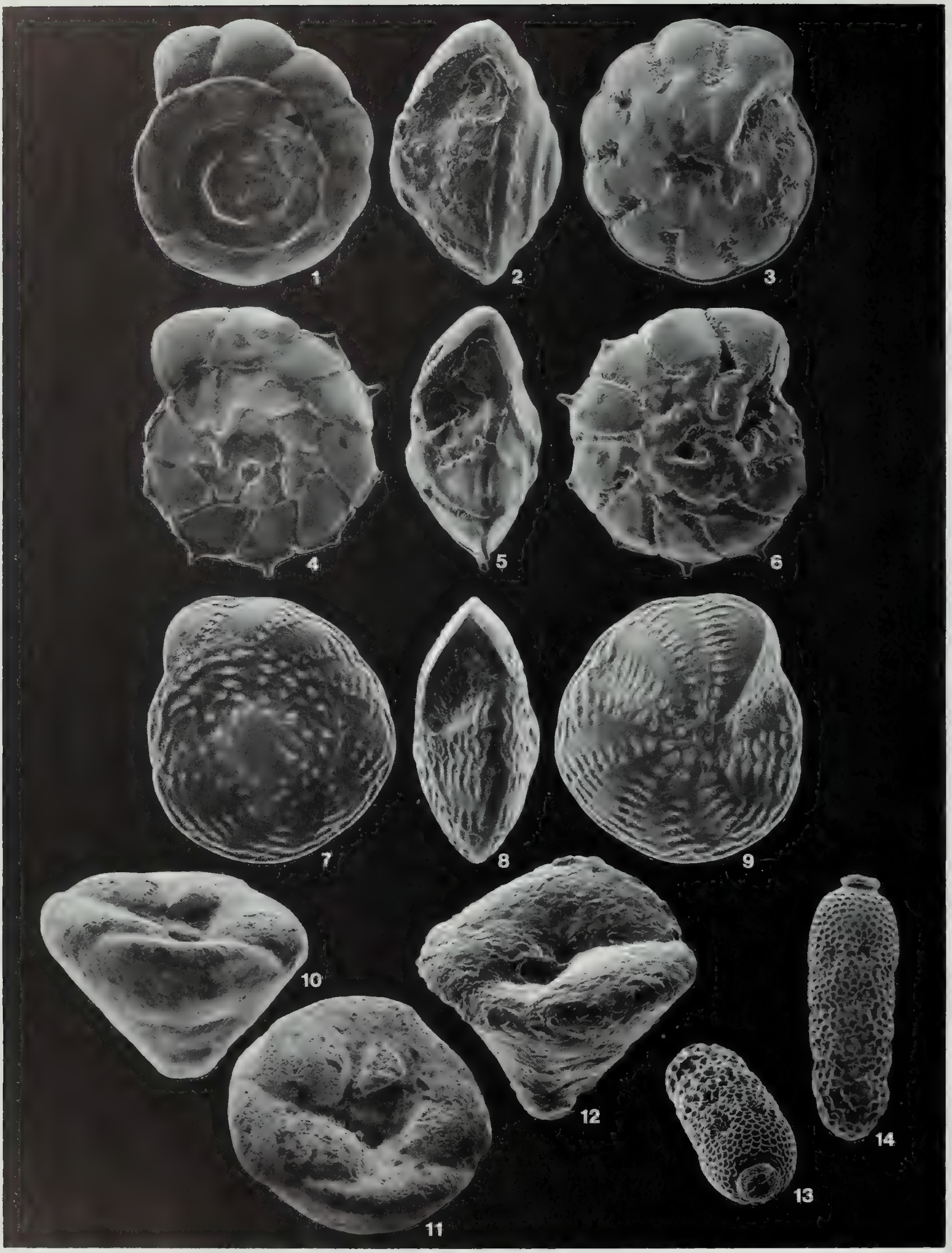
Trochammina irregularis (d'Orbigny) var. *clavata* Jones & Parker, 1860

LECTOTYPE. Designated by Kaminski *et al.* (in press), ZF4873. See below. From Galita Island.

TYPE REFERENCE. Jones & Parker, 1860: 304. No figure, but see Carpenter *et al.* 1862: pl. 11, fig. 6.

LOCALITIES. Recent; in the Mediterranean Sea, from 90 fathoms off Syra Island, also from 170 fathoms off Serpho (Seriphos) Island, and from 500 fathoms off Ipsara (Psara) Island; in 1100 fathoms between Crete and Santorin (Santorini or Thira) Island; also from 250 fathoms northwest of Crete; and 360 fathoms off Crete; between Malta and Crete in 1650 fathoms and in 1700 fathoms between Malta and the Grecian Archipelago.

REMARKS. Also recorded in the Catalogue as *Webbina clavata*. There are Recent syntypes from Ipsara (LII.1) 1894:4:3:615, from Syra (LIV.13) 1894:4:3:650 and from Serpho (LV.2) 1894:4:3:705. No specimens have been found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from Captain T.A.B. Spratt's dredging between Malta and Crete at 1650 fathoms (XLIX) 1884:4:3:586–590 or from Crete (LVII.1) 1894:4:3:748. There is an original note in the Recent Catalogue (p. 100, LXVIII), that the specimen from Spratt's dredging between Malta and the Archipelago (depth not given but it could be the 1700 fathoms reference), has been removed; it has not been subsequently located.

The lectotype, ZF4873, does not come from a locality specifically listed by Jones & Parker. Instead, Kaminski *et al.* (in press) selected another Mediterranean specimen from Galita Island off Tunis, S 22 W 32 miles, yellow mud, 320 fathoms, 38°00′N 9°13′E, collected at noon on 29th September 1859 by H.M.S. Firebrand (Catalogue p. 88, XLIII.'3', 6) 1894:4:3:507. In their opinion this specimen must have been available to the original authors at the time of their description and, by this definition, a syntype. It was chosen because it is the specimen figured by Carpenter *et al.* (1862: pl. 11, fig. 6), the first available figure of the species.

It is the type species of *Ammolagena* Eimer & Fickert.

Trochammina milioloides Jones, Parker & Kirkby, 1869

TYPE REFERENCE. Jones, Parker & Kirkby, 1869: 390; pl. 13, figs 9–14.

LOCALITIES. Fossil; Permian from the English localities of Sunderland, County Durham and Nosterfield, Yorkshire.

REMARKS. Specimens on (VI.1–3) P44797–9 from Sunderland (but they are not those figured) and others from Kirkby's material in H.B. Brady's collection, in the BM(NH), P35725, taken from the Permian Magnesian Limestone of Tunstal Hill, Sunderland can be regarded as syntypes. Slide (VI.4) P44800 from Yorkshire has not been located. On the slide registered P35725 there are, additionally, specimens of *Trochammina incerta* and *T. pusilla* which are superficially difficult to separate from this taxon. Patterson (1989: 94) considers *milioloides* to be a junior synonym of *Serpula pusilla* Geinitz, 1848.

Trochammina squamata Jones & Parker, 1860

'HOLOTYPE'. Redescribed by Hedley, Hurdle & Burdett 1964, 1963:2:19:1 (see below). From Crete.

TYPE REFERENCE. Jones & Parker, 1860: 304. No figure.

TYPE LOCALITY. Recent; from 360 fathoms, near Crete in the Mediterranean Sea.

REMARKS. Recorded as *Ammodiscus squamatus* in the Catalogue, p. 119. The specific diagnosis has been emended by Hedley, Hurdle & Burdett (1964: 419, 425, text-fig.1A, B; text-fig. 3, figs 1A, B and 3A–C). The single surviving, but umbilically damaged, specimen from the type locality (LVII.1) 1894:4:3:748 has been remounted and re-registered 1963:2:19:1. The type description provides no clue as to the number of specimens originally present in the sample, so why Hedley *et al.* considered this specimen as the holotype is unclear. They also found other uncatalogued specimens from 'off Galita Island, off Tunis 320 fathoms' (Catalogue: 88, XLIII.'3', 1–30) which have been remounted and re-registered as 1963:2:19:2–4.

Brönnimann & Whittaker (1988: 57) place *Trochammina squamata,* as redescribed by Hedley *et al.* 1964, into *Tritaxis* on account of its interiomarginal aperture and planoconvex test with 3+ chambers in the final whorl. They also state that most subsequent records of *T. squamata* are of other species.

Trochammina squamata Jones & Parker var. ***charoides*** Jones & Parker, 1860

LECTOTYPE. Designated by Berggren & Kaminski 1990, ZF4875. From Gorgo Island.

TYPE REFERENCE. Jones & Parker, 1860: 304. No figure.

LOCALITIES. Recent; from various localities in the Mediterranean sea: 90 fathoms off Syra Island, from off Serpho (Seriphos) Island, from 500 fathoms off Ipsara (Psara) Island, and from 1100 fathoms between Crete and Santorin (Santorini or Thira) Island, Grecian archipelago; also from 360 fathoms near Crete and 1700 fathoms between Malta and the Grecian Archipelago.

REMARKS. In the Recent Catalogue it is variously referred to as *Ammodiscus charoides*, from Serpho Island, 170 fathoms (Catalogue: 114, 115, LV), and from near Crete 360 fathoms (p. 119, LVII); as *Trochammina charoides* (pp. 94, XLV) from Gozo Island, and (p. 104, LII) from near Ipsara 500 fathoms; and as *Webbina charoides* (p. 105, LIII), from N.W. of Crete, 250 fathoms. From the remaining localities Jones was not able to recognize it. Berggren & Kaminski (1990) have designated a lectotype (ZF4875) from (XLV.5, 3) 1894:4:3:540 from a slide labelled 'Gorgo Island', which the Catalogue (p. 94) localizes at 'Cape Demetri (Gozo Island) S 63°E 33 miles, 704 fathoms, yellow tenacious mud, lat. 36°18′N long. 13°33′E, collected by H.M.S. Firebrand (J. Dayman, Commander) at 2 p.m. on 3rd October 1859'. It was chosen because it was believed to be the specimen illustrated by Carpenter *et al.* (1862: pl. 11, fig. 4), itself the first available figure of the species, but whose locality is not recorded. (Also see remarks under *T. irregularis* var. *clavata*, above, about the availability of H.M.S. Firebrand material).

This is the type species of *Repmanina* Suleymanov, which is

PLATE 3

Figs 1–3 *Rotalia beccarii* (Linnaeus) var. *annectens* Parker & Jones. Lectotype ZF4923, here designated; Hong Kong. Dorsal, edge and ventral views, respectively, × 70.

Figs 4–6 *Rotalia beccarii* (Linnaeus) var. *dentata* Parker & Jones. Lectotype ZF4925, here designated; Bombay harbour. Dorsal, edge and ventral views, respectively, × 70.

Figs 7–9 *Rotalia beccarii* (Linnaeus) var. *craticulata* Parker & Jones. ZF4926; Fiji Is. Dorsal, edge and ventral views, respectively, × 70.

Figs 10–12 *Valvulina triangularis* d'Orbigny var. *conica* Parker & Jones. Figs 10–11, P52791, from the Eocene of Hauteville, France. Fig. 10, edge (side) view; Fig. 11, ventral (apertural) view, showing the valvulinid tooth; both × 35. Fig. 12, ZF4928; Norway. Oblique side view showing the areal aperture of *Trochamminella*, × 90.

Figs 13, 14 *Uvigerina* (*Sagrina*) *dimorpha* Parker & Jones. Lectotype ZF4927, here designated; Abrolhos bank. Oblique-apertural and side views, respectively, × 100.

All scanning electron photomicrographs.

regarded by Charnock & Jones (1990: 158) as a subjective junior synonym of *Usbekistania* Suleymanov.

Trochammina squamata Jones & Parker var. ***gordialis*** Jones & Parker, 1860

Neotype. The so-called 'lectotype' selected from off Gozo in the Mediterranean, by Berggren & Kaminski 1990, ZF4876, is in fact the neotype: see p. 48.

Type reference. Jones & Parker, 1860: 304. No figure.

Localities. Recent; from the Arctic and Indian seas.

Remarks. There are no strict syntypes. Berggren & Kaminski (1990) found material collected by H.M.S. Firebrand in 1859 from the Mediterranean labelled '*Trochammina gordialis* (?) broken' on (XLV.5,3) 1894:4:3:540, from which they have selected a 'lectotype' (re-registered ZF4876). This taxon is not recorded from the Mediterranean in the type reference, but Jones identified it in his Catalogue as *Ammodiscus*, p. 115, (LV.6) or *Trochammina*, pp. 88, 95, 97, 99 & 103 solely from the Mediterranean and South Atlantic (p. 148); there is nothing from the 'Arctic and Indian seas'. Since the Firebrand material, even if to hand at the time of publication, is also not syntypic, the so-called lectotype is, according to Article 74a (v) of the ICZN, strictly a neotype and is designated such herein. Berggren & Kaminski (1990) argue that the specimen is most like the generally accepted concept of the species which serves to stabilize the nomenclature, and the selection is warranted since this species is, by its original designation, type species of *Glomospira* Rzehak. They also consider that this material was available to Jones & Parker (1860: 300, see footnote *) at the time of the original description and should therefore be considered syntypic. I beg to differ, but would not criticize the need to stabilize the concept of this species. They selected additional specimens as 'metatypes' (not a category recognized by ICZN), from Serpho (LV.6) 1894:4:3:709.

Truncatulina mundula Brady, Parker & Jones, 1888

Lectotype. Designated by Loeblich & Tappan 1955, ZF3585. From Abrolhos Bank.

Type reference. Brady, Parker & Jones, 1888: 228; pl. 45, fig. 25a–c.

Type locality. Recent; from a sounding: mud, tenacious olive-brown clay at 'Plumper' station 4, 22°54'S 40°37'W, 260 fathoms over the Abrolhos Bank off the coast of Brazil, South America.

Remarks. A lectotype (ZF3585) from (LXXXV.14) 1894:4:3:1038 was designated by Loeblich & Tappan (1955: 25; pl. 4, fig. 4) and apparently redesignated in 1964 (Fig. 621.1); paralectotypes were re-registered as ZF3584.

It is the type species of *Cibicidoides* Thalmann. It has not been recorded by Boltovskoy (1976) from the North Brazilian Sub-Province which includes the Abrolhos Bank.

Uvigerina (Sagrina) dimorpha Parker & Jones, 1865

Pl. 3, figs 13, 14

Lectotype (here designated). From Abrolhos Bank (*ex* 1894:4:3:1044), ZF4927.

Type reference. Parker & Jones, 1865: 364; pl. 18, fig. 18.

Localities. Recent; from 260 fathoms over the Abrolhos Bank, off Brazil, 22°54'S 40°37'W; also from near the Island of Shadwan, at 372 fathoms off SE point, entrance of Jubal Strait in the Red Sea [The Island of Shadwan is quoted by Jones (Catalogue p. 156) as being in the Gulf of Suez (LXXXIX)]; and from coral reefs, 17 fathoms, Australia (possibly Jukes' dredging no. 1; for details see Catalogue (p. 228, CIX) and see also under *Lagena sulcata* var. *distomapolita*, p. 51).

Remarks. Recorded in the Recent Catalogue as *Sagrina dimorpha*, there are syntypes from Abrolhos Bank, (LXXXV.20) 1894:4:3:1044 (from which the lectotype has been selected), and a variety from (LXXXV.35) 1894:4:3:1059. No specimens from the other localities have been recorded or yet located.

Uvigerina (Sagrina) raphanus Parker & Jones, 1865

Lectotype. Designated by Loeblich & Tappan 1964, ZF3582. From Indian Ocean.

Type reference. Parker & Jones, 1865: 364; pl. 18, figs 16, 17.

Localities. Recent; from the West Indies and Panama; from India on a clam shell, also from anchor mud in Bombay harbour, India; from anchor mud at Hong Kong, China; and from coral reefs, 17 fathoms, Australia.

Remarks. Recorded in the Recent Catalogue as *Sagrina raphanus*. There are syntypes from the Indian Ocean, (XCIII.38) 1894:4:3:1366, from off the shells of *Chama hippopus* (=*Hippopus maculatus*); the precise geographical locality is not given. It is from this slide that Loeblich & Tappan (1964: C553) designated, but did not figure, a lectotype (ZF3582). This and paralectotypes (ZF3581) were examined by Whittaker & Hodgkinson (1979: 56) and no completely uniserial forms were found. Other paralectotypes, which were part of an exchange, are deposited in the National Museum of Natural History (Smithsonian Institution), Washington. There are also Canada balsam mounts from these clam shells (1894:4:3:2008, 2030 and 2032). Other specimens are present from Hong Kong anchor mud, (XCVI.6) 1894:4:3:1465, but none have yet been found from the remaining localities mentioned above.

Whittaker & Hodgkinson (1979: 56) consider the lectotype and paralectotypes to belong in *Rectobolivina* Loeblich & Tappan 1964, since the type of this genus, *Sagrina bifrons* Brady, is biserial in both generations, then later rectilinear with toothplates alternating at 180°.

Valvulina mixta Parker & Jones, 1865

Lectotype. Designated by Loeblich & Tappan 1964, ZF3591. From Melbourne.

Type reference. Parker & Jones, 1865: 438 and table 10.

Type figure. Carpenter *et al.* 1862: pl. 11, figs 19, 20, 25, 26.

Type locality. Recent; from coast sand, Melbourne, Australia.

Remarks. Syntypes are present on (CIII.45–7) 1894:4:3:1565–1568. A lectotype was designated but not figured by Loeblich & Tappan (1964: C279–281), ZF3591 (*ex*

1894:4:3:1565); paralectotypes are on ZF3590 (*ex* 1894:4:3:1563, 1565 and 1566). Their figured specimens are probably amongst those exchanged with the National Museum of Natural History, Washington. The 1894:4:3:1563 specimens are recorded in the Catalogue as *Valvulina triangularis* d'Orbigny.

Valvulina mixta is the type species of *Cribrobulimina* Cushman. Loeblich & Tappan (1988: 182) rescinded their former remarks (1964: C279), on the validation of authorship, in which they claimed Parker & Jones' taxa *mixta* and *polystoma* were *nomina nuda*.

Valvulina polystoma Parker & Jones, 1865

LECTOTYPE. Designated by Loeblich & Tappan 1964, ZF3593. From Melbourne.

TYPE REFERENCE. Parker & Jones, 1865: 437–8 and table 10.

TYPE FIGURE. Carpenter *et al.* 1862: pl. 11, figs 21, 24.

LOCALITIES. Recent; from Australia, at 7 or 8 fathoms, white shelly mud at Swan River; and from coast sand at Melbourne.

REMARKS. A lectotype was designated by Loeblich & Tappan (1964: C279–81), ZF3593 (CIII.41, *ex* 1894:4:3:1562), from the shore sand at Melbourne; the paralectotypes have been re-registered as ZF3592. These specimens were recorded as *Valvulina triangularis* in the Catalogue (p. 222: CIII.39–44). On (p. 218: CI.7) 1894:4:3:1516, the only record from Swan River, 7 or 8 fathoms, is a buliminoid form labelled '*Valvulina* ?'.

V. polystoma is considered a senior synonym of *Valvulina mixta*, the type species of *Cribrobulimina*, by Loeblich & Tappan (1988: 182), since both forms merely represent different degrees of development of the multiple aperture.

Valvulina triangularis d'Orbigny var. ***conica*** Parker & Jones, 1865

Pl. 3, fig. 10–12

TYPE REFERENCE. Parker & Jones, 1865: 406; pl. 15, fig. 27a, b.

LOCALITIES. Fossil; from the Tertiary of Grignon and Hauteville, France.

Recent; from 30–200 fathoms off the coast of Norway between North Cape and Drontheim, 69°–63°N lat. (Locality VIII); also from Galita Island S 32 W 32 miles, 38°00′N 9°13′E, in the Mediterranean Sea; from the Abrolhos Bank off Brazil at 47 fathoms, 23°02′S 41°02′W, in the South Atlantic Ocean; and in coast sand, Melbourne, Australia.

REMARKS. In the Fossil Catalogue there are no records under any combination of name from Grignon, neither were they found there by Le Calvez (1970). However, *Valvulina conica* is listed from Hauteville (Hautteville), Département Manche, France (LXXIX.50–60) P47237–47 (one specimen is figured here on Pl. 3, figs 10, 11 and re-registered as P52791), but these specimens are not here considered congeneric with the original figure since they have the typical valvular tooth of *Valvulina* and are much larger. No syntypes are recorded in the Recent Catalogue, but as Parker & Jones figured the variety from Norway Locality VIII, I carefully examined these slides. On one of them, (XXVI.14) 1894:4:3:239, I found a single, unidentified specimen which is very like that illustrated by Parker & Jones (1865: pl. 15, figs 27a, b); this specimen ZF4928 is illustrated here, but cannot be designated lectotype since my identification is subjective (see p. 48). The aperture is interio-areal, thus placing it in the genus *Trochamminella* Cushman (J.E. Whittaker, personal communication). Carpenter's *Valvulina*, from an unknown locality, figured (Carpenter *et al.* 1862: pl. 11, figs 16, 23) and considered synonymous in the type description, appears to have an interiomarginal aperture and is not here regarded as congeneric.

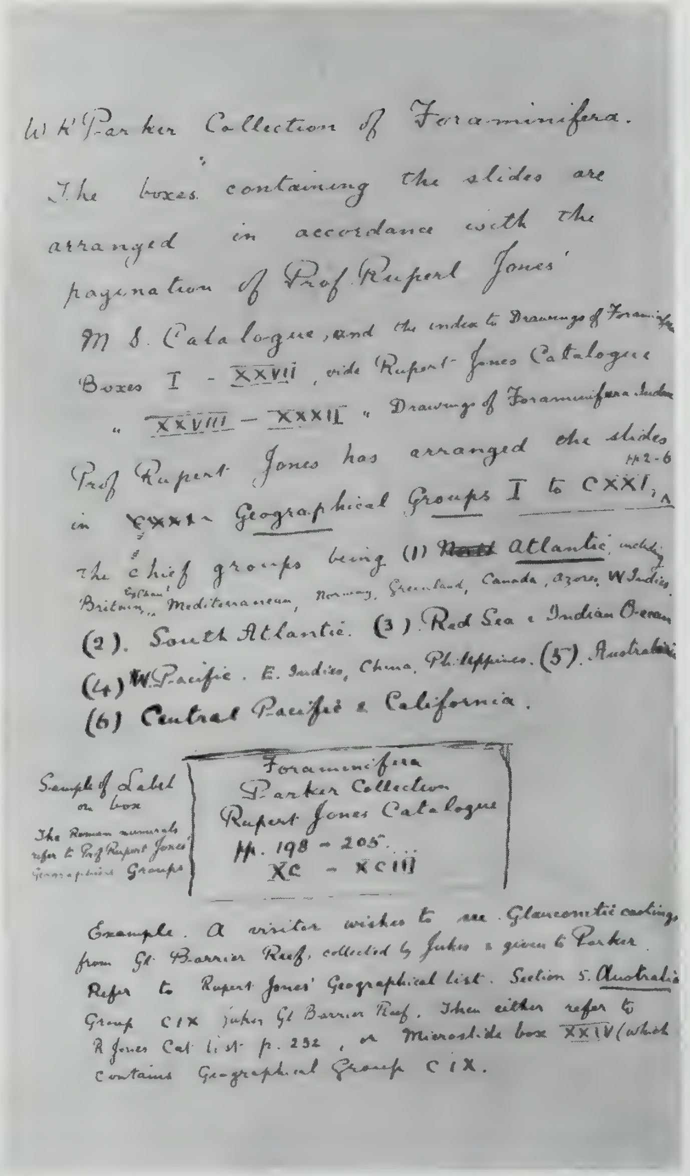
WILLIAM KITCHEN PARKER: A SHORT BIOGRAPHY

He was born on 23rd June 1823, in an old farm house with a beautiful garden in the hamlet of Dogsthorpe within the Parish of Paston, 2 miles north-east of Peterborough, Northamptonshire, England. He was the second son to survive (six little ones died in infancy) and youngest child of Thomas Parker, a Wesleyan of the old school, 'a Methodist-Churchman' yeoman farmer. His mother Sarah (née Kitchen) was a farmer's daughter.

He was first taught at a 'dame school' in the village at Dogsthorpe and later at the Parish schools of Werrington and Paston. This was all his father deemed necessary for, as a farmer's son, the intervals in school time were filled with work on the farm. At the age of 14, dispirited by the drudgery of farm work, he asked his father if he could return to school to train himself either as a bookseller or a lawyer. He was sent for three short quarters (nine months) to Peterborough Grammar School, under the headmastership of the Rev. William Cape. There he learnt, in a crash course, all the Latin and Greek he ever knew.

At 15 years of age he wanted nothing more to do with farming so he began an apprenticeship with Mr Woodroffe, a chemist and druggist in Stamford. Although working a 15 hour day, from 7 a.m. to 10 p.m., he was an early riser; in summer at 4 a.m. Dragging fellow apprentice Jack Day in his wake, he would engage in botanical forays in the Fenlands during the hours before breakfast, often returning exhausted before the day's work. Over a two year period he collected and named more than 500 species of plants, in which he had an ardent supporter in the Rev. Samuel Walker. He read as much as possible in his spare time. Three years later, at 18, when Mr Woodroffe had taught him all he could, he was released from his indenture to go to Mr Costal, a medical practitioner at Market Overton in Rutland. There over the next two years he acquired the rudiments of surgery and human anatomy. During the holidays he kept pets, and forced himself to dissect many dead animals (a donkey and birds), a task distasteful to him. He prepared and drew skeletons, especially those of birds.

He was never to have a University education, but his good memory, manual dexterity and ability to draw were natural talents. Under circumstances now shrouded by time, he left for London in 1844. Between the December of that year and 1846 he studied at King's College, London, becoming a student demonstrator (a Prosector), first to Dr Robert Bentley Todd (later Professor), an Irishman who never understood his ways of learning, and then to Mr (later Sir William) Bowman, an Englishman who understood him better and became a life long friend. During this time he lodged, as a



W K Parker Collection of Foraminifera.

The boxes containing the slides are arranged in accordance with the pagination of Prof. Rupert Jones' MS. Catalogue, and the index to Drawings of Foraminifera

Boxes I - XXVII, vide Rupert Jones Catalogue

" XXVIII - XXXII " Drawings of Foraminifera Index

Prof Rupert Jones has arranged the slides in ~~CXXI~~ Geographical Groups I to CXXI, pp. 2-6

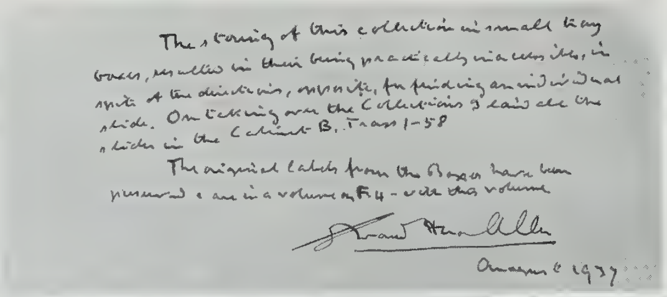
the chief groups being (1) ~~North~~ Atlantic, including Britain, England, Mediterranean, Norway, Greenland, Canada, Azores, W Indies. (2). South Atlantic. (3). Red Sea & Indian Ocean (4) W. Pacific. E. Indies, China, Philippines. (5). Australia (6) Central Pacific & California.

Sample of Label on box

The Roman numerals refer to Prof Rupert Jones' Geographical Groups

Foraminifera
Parker Collection
Rupert Jones Catalogue
pp. 198 - 205.
XC - XCIII

Example. A visitor wishes to see Glauconitic castings from Gt. Barrier Reef, collected by Jukes & given to Parker. Refer to Rupert Jones' Geographical list. Section 5. Australia Refer to Group CIX Jukes Gt Barrier Reef. Then either refer to R Jones Cat list p. 232, or Microslide box XXIV (which contains Geographical Group CIX.

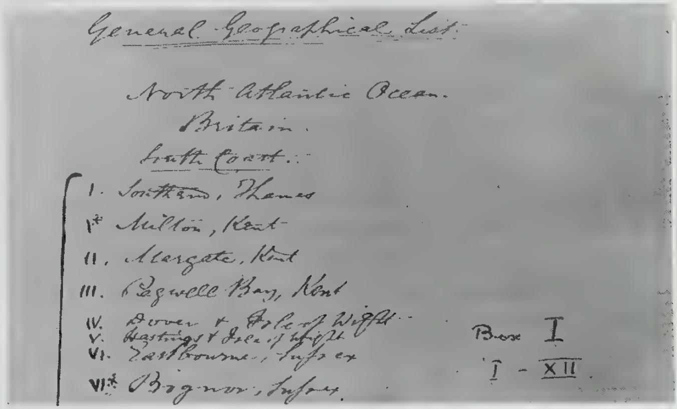


The storing of this collection in small tiny boxes, resulted in their being practically inaccessible, in spite of the directions, opposite, for finding an individual slide. On taking over the Collections I laid all the slides in the Cabinet B. Trays 1-58

The original labels from the Boxes have been preserved & are in a volume on F4 - with this volume

Edward Heron-Allen

[illegible] 6 1937

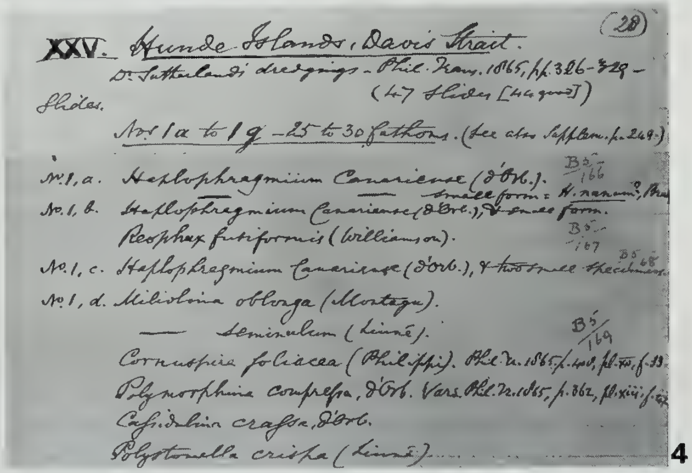


General Geographical List.

North Atlantic Ocean.
Britain.
South Coast.

- I. Southend, Thames
- I* Milton, Kent
- II. Margate, Kent
- III. Pegwell Bay, Kent
- IV. Dover & Isle of Wight
- V. Hastings & Isle of Wight
- VI. Eastbourne, Sussex
- VI* Bognor, Sussex.

Box I
I - XII



(28)

XXV. Hunde Islands, Davis Strait.
Dr Sutherland's dredgings - Phil. Trans. 1865, pp. 326-329 -
(47 Slides [44 good])

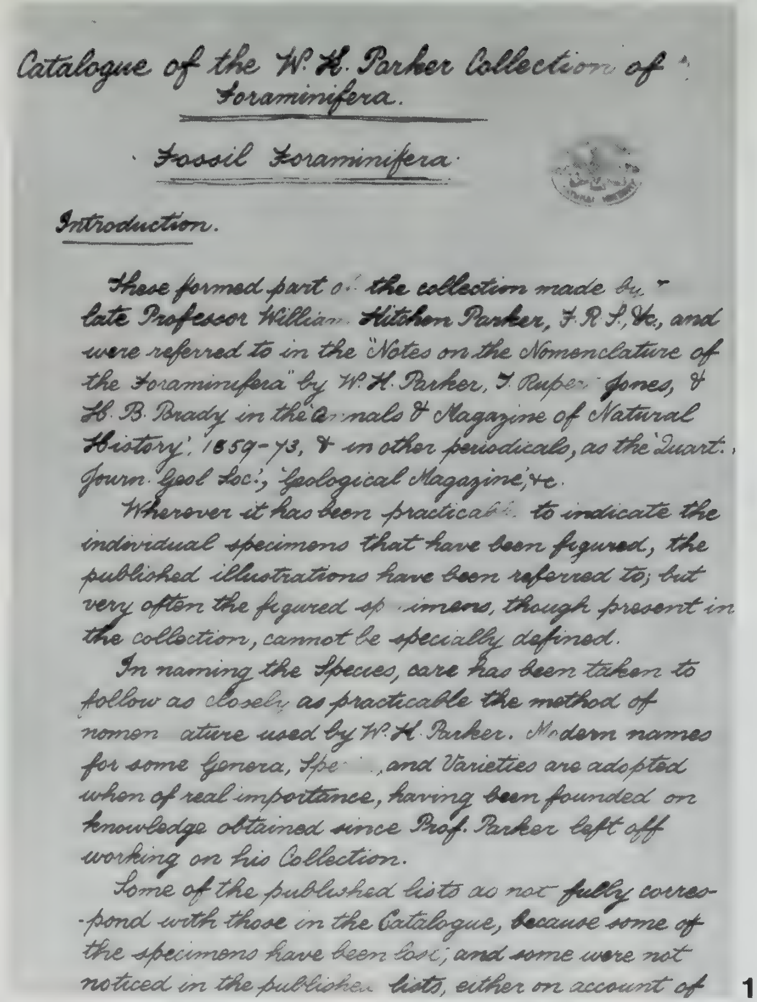
Slides.

Nos 1a to 1g - 25 to 30 fathoms. (See also Supplem. p. 249.)

No. 1, a. Haplophragmium Canariense (d'Orb.). B5/166
— small form = H. nanum?
No. 1, b. Haplophragmium Canariense (d'Orb.), ~~& small form~~.
Reophax fusiformis (Williamson). B5/167
No. 1, c. Haplophragmium Canariense (d'Orb.), ~~& two small specimens~~. B5/168
No. 1, d. Miliolina oblonga (Montagu).
— seminulum (Linné). B5/169
Cornuspira foliacea (Philippi). Phil. Tr. 1865, p. 408, pl. xv, f. 33
Polymorphina compressa, d'Orb. Vars. Phil. Tr. 1865, p. 362, pl. xiii, f.
Cassidulina crassa, d'Orb.
Polystomella crispa (Linné)

PLATE 4

Figs 1–4 Extracts from the Jones' Recent Catalogue. Fig. 1, introductory page. Fig. 2, Edward Heron-Allen's note in 1937, justifying rehousing in slide drawers. Fig. 3, a portion of the General Geographical List. Fig. 4, a locality number with details and faunal content of four slides.



Catalogue of the W. K. Parker Collection of Foraminifera.

Fossil Foraminifera.

Introduction.

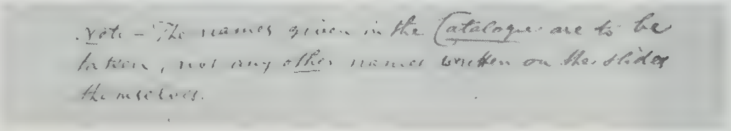
These formed part of the collection made by the late Professor William Kitchen Parker, F.R.S., &c., and were referred to in the "Notes on the Nomenclature of the Foraminifera" by W. K. Parker, T. Rupert Jones, & H. B. Brady in the Annals & Magazine of Natural History, 1859–73, & in other periodicals, as the 'Quart. Journ. Geol. Soc.', 'Geological Magazine', &c.

Wherever it has been practicable to indicate the individual specimens that have been figured, the published illustrations have been referred to; but very often the figured specimens, though present in the collection, cannot be specially defined.

In naming the Species, care has been taken to follow as closely as practicable the method of nomenclature used by W. K. Parker. Modern names for some Genera, Species, and Varieties are adopted when of real importance, having been founded on knowledge obtained since Prof. Parker left off working on his Collection.

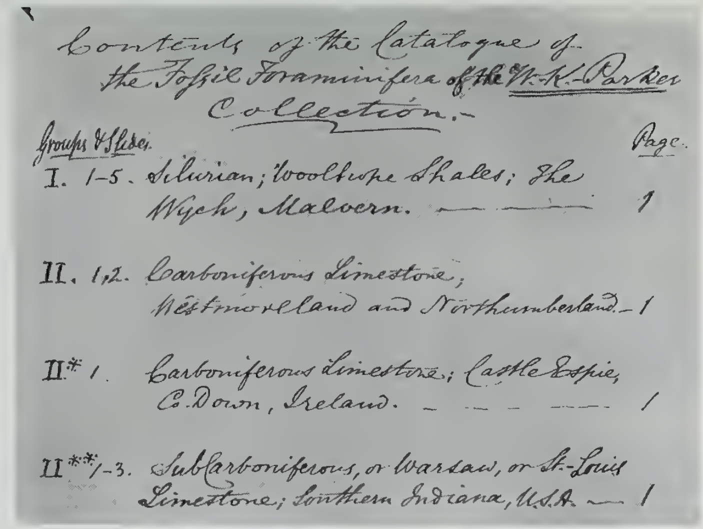
Some of the published lists do not fully correspond with those in the Catalogue, because some of the specimens have been lost; and some were not noticed in the published lists, either on account of

1



Note – The names given in the Catalogue are to be taken, not any other names written on the slides themselves.

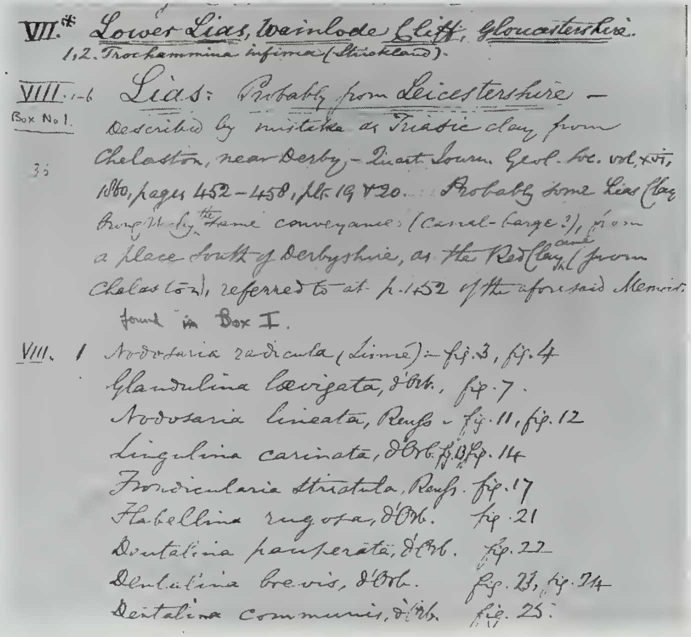
2



Contents of the Catalogue of the Fossil Foraminifera of the W. K. Parker Collection.–

Groups & Slides.		Page.
I. 1-5.	Silurian; Woolhope Shales; The Wych, Malvern.	1
II. 1,2.	Carboniferous Limestone; Westmoreland and Northumberland.	1
II.* 1.	Carboniferous Limestone; Castle Espie, Co. Down, Ireland.	1
II.** 1-3.	SubCarboniferous, or Warsaw, or St. Louis Limestone; Southern Indiana, U.S.A.	1

3



VII.* Lower Lias, Wainlode Cliff, Gloucestershire.
1,2. Trochammina infima (Strickland).

VIII. 1-6 Box No 1. Lias: Probably from Leicestershire – Described by mistake as Triassic clay, from Chelaston, near Derby, – Quart. Journ. Geol. Soc. vol. xvi, 1860, pages 452–458, pls. 19 & 20. Probably some Lias Clay brought by the same conveyance (Canal-barge?), from a place South of Derbyshire, as the Red Clay and Marl (from Chelaston), referred to at p.452 of the aforesaid Memoir. found in Box I.

35

VIII. 1 Nodosaria radicula (Linné) – fig.3, fig.4
Glandulina laevigata, d'Orb., fig.7.
Nodosaria lineata, Reuss – fig.11, fig.12
Lingulina carinata, d'Orb. fig.13, fig.14
Frondicularia striatula, Reuss. fig.17
Flabellina rugosa, d'Orb. fig.21
Dentalina pauperata, d'Orb. fig.22
Dentalina brevis, d'Orb. fig.23, fig.24
Dentalina communis, d'Orb. fig.25.

4

PLATE 5

Figs 1–4 Extracts from the Fossil Catalogue made by T. Rupert Jones. Fig. 1, Part of the Introduction. Fig. 2, confirmation that only the Catalogue names are correct, not the identifications written on the slides. Fig. 3, part of the Catalogue contents list. Fig. 4, a locality number with locality details and faunal content of part of one slide.

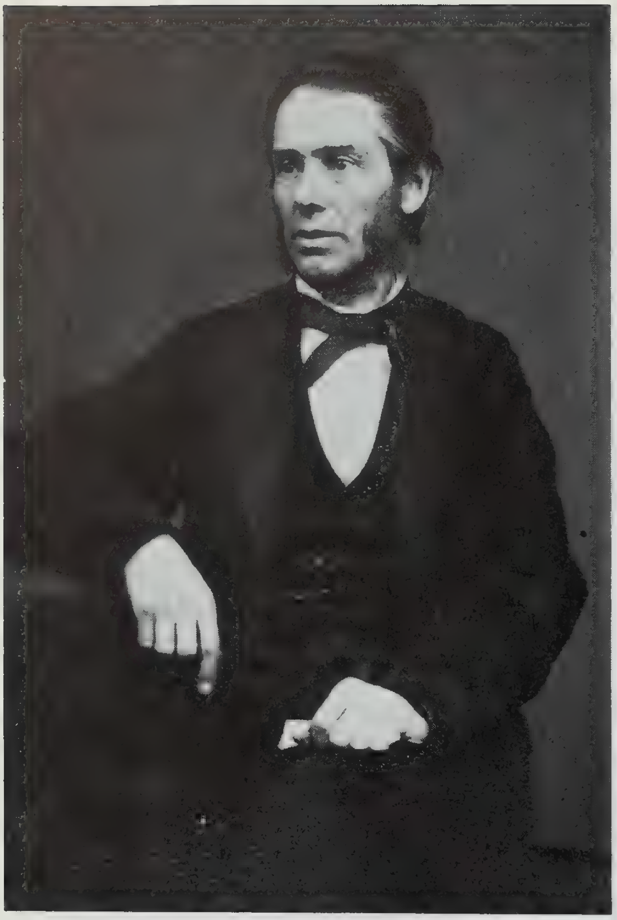


Fig. 4 William Kitchen Parker, 1823–1890. Reproduced, with permission, from a photograph in the possession of Newcastle-upon-Tyne City Libraries & Arts, H.B. Brady archive.

'resident assistant', with the family of Mr Booth, a general practitioner in Little Queen Street, Westminster, whose lives he tended to enliven. He attended Charing Cross Hospital as a medical student in 1846 and 1847, and a private school in Bedford Square. He worked hard until 5 p.m., then often reading a philosophical book he would walk along The Strand to his lodgings, where he read his Bible for an hour before going out to prayer sessions, class meetings or visiting the sick.

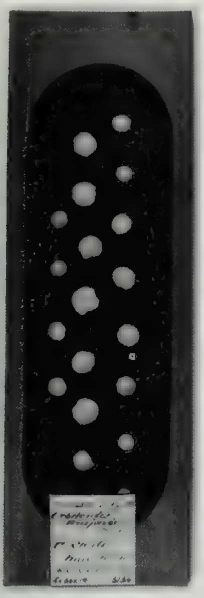
During his student life he met a Miss Elizabeth Jeffrey (born 18th February 1825), youngest daughter of Thomas Jeffrey, then Clerk to the Vauxhall Bridge Company. They became engaged in 1849, and having qualified as a Licentiate of the Society of Apothecaries, he commenced practice as a doctor in the same year at 124 Tachbrook Street, Pimlico, London. He was then 26. On his meagre earnings supplemented by his patrimony they were able to marry on 1st January 1850, at St John's, Westminster. After 2 or 3 years of prosperity he moved with his growing family to 18 Bessborough Street, and some twelve years later to 36 Claverton Street, S.W. London. During this time he became interested and skilled in midwifery and was a medical adviser to the Westminster Training College for Teachers. When he finally retired in 1883 he moved to a pleasant house he called 'Crowland' in Trinity Road, Upper Tooting, and later to a smaller one in Hendham Road, where on his reduced income and small Civil List pension he felt calmer and freer than he had been for many years. Surrounded by his research projects and spirit-preserved collection he was happy. At this later period of life he rose late and retired early (the antithesis of his youthful days) and dozed after dinner. He worked in the morning and until his last years wrote for 2 hours in the evening, never seeming to hurry but achieving more than most would in the same time.

He was intensely devoted to his wife and family, but about them his son Thomas Parker (1893) says almost nothing. His wife bore him four sons and three daughters, and being calm and unflustered managed him well throughout their life together. She predeceased him by about 4 months (dying on the 10th March 1890) and he was greatly shaken by her death, suffering an *angina pectoris* attack soon after, from which he appeared at first to make a good recovery. Of their offspring, the first, Thomas Jeffery (1850–1897) became Professor of Zoology and Comparative Anatomy in the University of Otago, New Zealand. His election as a Fellow of the Royal Society (of England) was confirmed posthumously. The second, William Newton, was Professor of Biology at the University College at Cardiff and died in 1923. His other sons are, to me, more shadowy; the third, an able draughtsman and lithographer (this must be M.P.), and the fourth, at the time of his father's death, had just taken his English medical diplomas of L.R.C.P and M.R.C.S. (this must be another W.K.). About the daughters I have no information at this time.

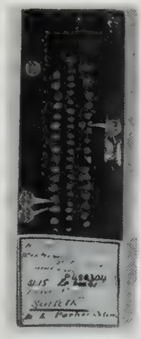
Thomas Parker (1893) illustrates his book with a frontispiece of his father, but remarks that the best portrait he ever saw was a large full-length photograph taken by Hering of Regent Street when he was about 45 years old. With the exception of those in the Album for Sir J. Murray (Crane 1897; 14 number 3, centre), one in the Presidental Gallery of the Royal Microscopical Society (Anon. 1885) and the one (Fig. 4), reproduced here by permission of the Newcastle-upon-Tyne City Libraries and Arts (from their H.B. Brady archive), no others have been traced. He was about 5 feet 9 inches (1.74 m) tall, large boned, sparsely and rather loosely built ('frail and weakly') and before he turned grey in his middle years his hair was nearly black and brushed back from his square forehead. His mouth had a slightly projecting lower lip with white and regular front teeth and his chin was rounded, deeply cleft or dimpled. His eyes were dark brown, wonderfully bright and expressive. His hands were long and bony but slender and slim fingered. He walked rapidly with much swinging of arms and legs and his movements were quick and nervous (Parker 1893). He was variously excitable with high swings between euphoria and depression, energetic, with a rapidly working mind, good memory and concentration level. His handwriting, from letters preserved in the Royal Society archives, performed with a fine nibbed pen, was appalling. He was courteous, upright, large hearted,

PLATE 6

Figs 1–17 Curation and labelling of the Parker Collection. Fig. 5, one of the original storage boxes which still bears original labels and trays. Figs 1–4, 6–9, 11–13 & 16, a selection of slides. Figs 4, 13, tubes on slides. Fig. 10, a large specimen. Fig. 15, a pill box. Figs 14, 17, tablets.



1



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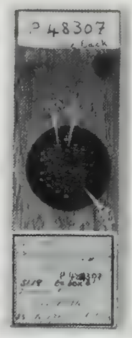
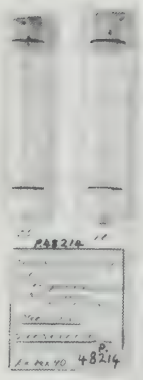
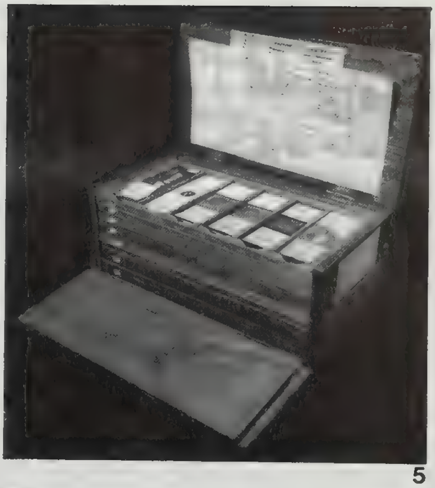


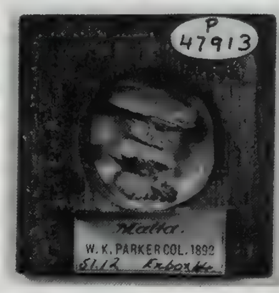
3


P48214
P.
48214

4

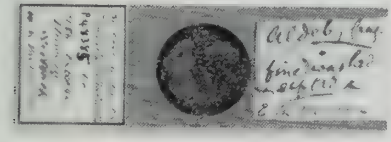


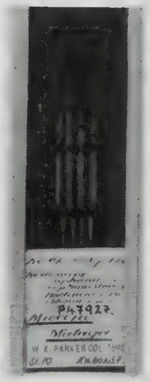
5


P
47913
Malta.
W. K. PARKER COL. 1892
Sl.12 Ex box 44

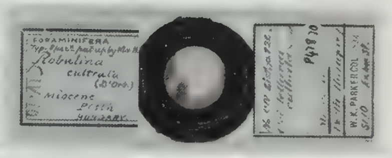
6

7

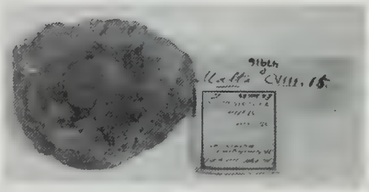



P47927
Miocene
W. K. PARKER COL 1892
Sl.10 Ex box 37

8

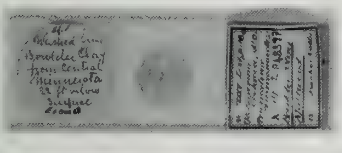

FORAMINIFERA
Robulina
cultrata
(D'Orb.)
Miocene
Pesth
HUNGARY
P43870
W. K. PARKER COL
Sl.10 Ex box 37

9

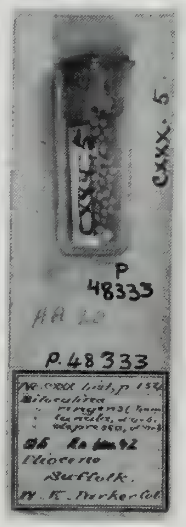

Malta
CVIII. 15.

10

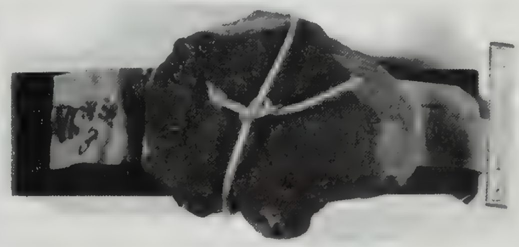
11


Washed from
Boulder Clay
from Central
Minnesota
22 ft below
Surface

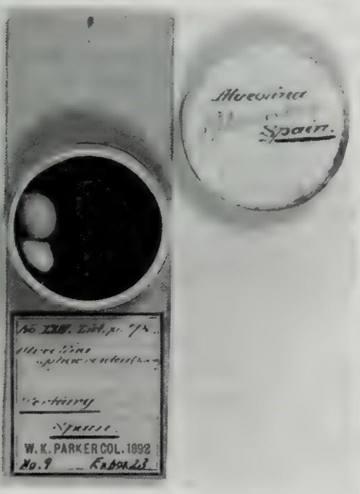
12


CXXX. 5
P
48333
P.48333
Biloculina
Pliocene
Suffolk.
W. K. Parker Col.

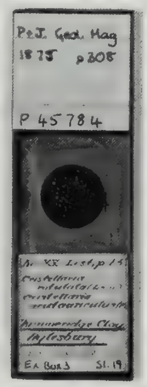
13



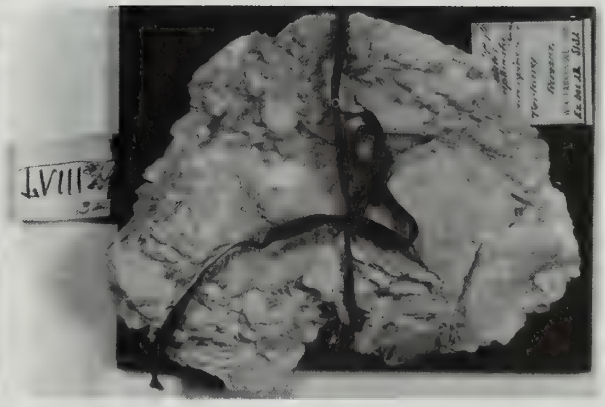
14


Alveolina
Spain.
Tertiary
W. K. PARKER COL. 1892
No. 9 Ex box 23

15


P.J. Geol. Mag
1875 p 308
P 45784
Kimmeridge Clay
Aylesbury
Ex Box 3 Sl. 19

16



17

gentle by nature, cheerful with a sweet and winning smile, popular with his patients, modest, conscientious, conservative to a degree, 'an unworldly seeker after truth', unselfish, being generous to fellow workers and most patient and helpful to youngsters, identifying their specimens and giving information. He did not try to attract rich clients and his consulting room was like a laboratory in its appearance. He lived plainly without extravagance and dressed as shabbily as was allowable for a physician. He was a good father, earnest in business and such a hard worker that he was compelled for a time, at one period (unspecified), to give up some of his practice. Throughout his adult life he suffered constant ill health, never passing a day without pain or enjoying an unbroken night's rest. His unspecified ailments, which might have been constant digestive troubles, were attributed at the time to his having outgrown his strength by growing 8 inches between the ages of 14 and 15, and in his late teens misusing his constitution by not eating properly so that he often had fainting fits. Often he did some of his best scientific work when unwell, as it provided him with a distraction from his discomfort. In 1856 and again in 1874 he had long and serious, but again unspecified, illnesses.

He liked reading the Bible and Shakespeare (the latter he discovered at the age of 23 and devoured), Milton, Spenser, Pope, Cowper and Tennyson (the love of whom he possibly acquired from his mother and her family who were keen readers), the early works of Eliot, biography and theology. He fervently admired Bacon, Bishop Butler and John Howe. He read all the best new books supplied from Mudie's. His sole professional reading was said to be the *British Medical Journal*. Surprisingly with his talent for learning he had little interest in the world at large; there was seldom a daily paper in the house apart from *The Athenaeum*. He disliked those 'heavier' reviews, like the *Quarterly* and *Edinburgh*, positively disliked Dickens and rarely read a second class novel. He had no more than a rudimentary interest in politics. He never, out of school, played a game, seldom went to the theatre, buildings of great beauty or picture galleries but delighted in walks on the common. He had little or no knowledge of the French or German languages nor was he apparently interested in foreign research prior to his own. He enthusiastically carried on his medical work and natural history studies but when lecturing he tended to be obscure and rambling. He was a great talker, monopolizing the conversation, then taking interested listeners into his study, afterwards complaining that they exhausted him; his family tried to control him by keeping the subject matter general.

Born into a Wesleyan family, he enjoyed a simple and firm Christian faith. During his fifteenth year he began to lead an intensely religious life for which he was later well known: he saw the Creator's hand everywhere and realised that however much he studied he would never understand everything, but would enjoy trying to do so. He tried to conduct unbiased single sighted research, following trails to their natural conclusions, considering that his duty was to learn from nature, comparing like with like and not attempting what he would call 'system-building'.

His main interests were his medical work, especially midwifery, which was his livelihood, and almost equally his natural history studies carried out in his 'den' or study at Claverton Street of which Bettany (1891) gives a good description. Those, for which he received his major accolades, were on anatomical research into cranial osteology and the systematic position of birds, sturgeon, sharks, Amphibia and the pig, as well as the development of the shoulder girdle and sternum in vertebrates. He also studied *Archaeopteryx* and other fossil birds and living green turtles. Most of his dissections and section making, at which he was most adept, were done by the naked eye or under the lens; he would not use a microtome or embedding bath. At the same time he also examined the microscopic structure of animal and vegetable tissues, Polyzoa and Foraminifera.

His interest in the Foraminifera, which was the only group in which he was to get beyond the mounting and naming stages, was kindled by examining sand collected on a visit to Bognor, Sussex, and from amongst sponge sand and sediment associated with Indian Ocean sea-shells. Having sorted, mounted and drawn numbers of these microzoa, he was induced by his friends, T. Rupert Jones (who lived nearby in Bessborough Gardens in the early 1850s) and W. Crawford Williamson around the year 1856, to work on Recent and fossil Foraminifera systematically. He was in great measure a self-taught man and a skilled draughtsman, but unfortunately he was a diffuse, obscure and rambling writer, without system. He never revised a manuscript, the first draft going to the printer to be modified only in minor detail at proof stage. These 'minor' details were not worth his trouble. His friend T.H. Huxley attempted to guide him, usually to no avail. He could never write readable articles and thus never did himself justice. He never catalogued his preparations, relying on his excellent memory which up to the very last was marvellous. The few notes he made were sketchy and seldom referred to, which explains why Jones had to compile the Catalogues to his Foraminifera collection after his death. He produced 95 publications, 36 being on the Foraminifera.

All this research brought him outside honours. He was elected Fellow of the Royal Society in 1865 (aged 42), on the recommendation of eight fellows amongst whom were T.H. Huxley, W.B. Carpenter and W.H. Flower. He received one of the two Royal Medals given annually by the Queen on the nomination of the Royal Society in 1866 and his letter of thanks is still on file in the Society's archives. The President, Edward Sabine, mentioned his work on Foraminifera but the award was really for his '. . . comprehensive, exact and useful researches in the developmental osteology and embryonal morphology of Vertebrates'. Later, in 1876, he received a Royal Society annual Government Grant Fund to aid his studies which after it had ceased was succeeded by a (Civil List) pension from the Crown. A generous friend from a Wesleyan family aided him with the heavy cost for plates, incurred in publishing in *Philosophical Transactions of the Royal Society*. In 1873 (aged 50), he received a diploma as Member of the Royal College of Surgeons, and a year later was appointed joint Hunterian Professor (with Professor Flower); he held the post until 1884. He was a Fellow of the Zoological (1864) and Linnean (1875) Societies (where in both cases, as a special compliment, the composition fee was remitted), and of the Royal Microscopical Society, of which he was elected President for the period 1871–1872 (given as 1871–1873 by T. Parker, 1893). He became an honorary member (a Fellow in 1875) of King's College London, and was associated with the Philosophical Society of Cambridge, the Medical Chirurgical Society, the Imperial Society of Naturalists of Moscow and the American Ornithologists' Union. He was a corresponding member of the Imperial Geological Institute of Vienna and the Academy of Natural Sciences of Philadelphia (Howes 1895). In 1885 (aged 62) he received the Baly Medal from the Royal College of Physicians. He was invited in 1874 to be a director of the Star Life Assurance Association, a remunerative position amongst friends which, once a week, took him out and away from his introspective research.

He died after lunch, peacefully at the age of 67 on 3rd July 1890, of 'syncope of the heart' whilst visiting his second son, Prof. W.N. Parker in Cardiff. He was buried in Wandsworth Cemetery, London, beside his wife, beneath a recumbent cross of red granite surrounded by a low, inscribed coping.

The major references to his life are: Allen (1890), Anon. (1885), Bell (1890), Bettany (1891), Crane (1897), Harting (1890), Howes (1895), Jones & Harting (1891) and T.J. Parker (1893), which can be found in the bibliography below. Much the same information can be found in the following: *The Times* of July 14th 1890; the *British Medical Journal* 1890: 116; *Nature,* July 24th 1890: 297–299; *The Ibis*, series 6, 2 (1890): 468–470 and *Proceedings of the Linnean Society*, Session 1890–91, October 1893: 26–27.

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Barremian–Aptian Praehedbergellidae of the North Sea area: a reconnaissance

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Synopsis. The taxa of the Praehedbergellidae which have been obtained from sediments of Barremian and Aptian age, in the off-shore North Sea area, include species of the genera *Praehedbergella* Gorbachik & Moullade, *Blefuscuiana* Banner & Desai and *Lilliputianella* Banner & Desai. The definitions of *Praehedbergella* and *Blefuscuiana* are modified to enhance their distinction.

Praehedbergella includes the taxa *P. grigelisi* (Banner & Desai) *perforare* n.subsp., *P. pseudosigali* n.sp., *P. ruka* n.sp. (including *P. ruka contritus* and *P. ruka papillata* n. subspp.), *P. sigali* (Moullade) *sensu lato, P. tuschepsensis* (Antonova) and *P.* cf *handousi* (Salaj). *P. sigali* has been recognised to comprise three subspecies: *P. sigali* s.s., *P. sigali compacta* n.subsp., and *P. sigali rasilis* n.subsp.

Blefuscuiana includes *B. aptiana* (Bartenstein) (including *B. aptiana depressa* n.subsp. and *B. aptiana implana* n.subsp.), *B. daminiae* n.sp., *B. excelsa* (Longoria) *cumulus* n.subsp., *B. gorbachikae* (Longoria), *B. laculata* n.sp. (including *B. laculata alobata* n.subsp.), *B. occulta* (Longoria) *sensu stricto, B. occulta* (Longoria) *perforocculta* n.subsp., *B. praesimilis* n.sp., *B. rudis* n.sp. and *B. whittakeri* n.sp. Metatypes of *B. infracretacea* (Glaessner) are redescribed and their first SEM images are given; *B. infracretacea s.s.* possesses strongly developed perforation cones, but *B. infracretacea aptica* (Agalarova) lacks them.

Lilliputianella includes *L. similis* (Longoria) and *L. eocretacea* (Neagu).

No species of planispiral praehedbergellids (e.g. of the genera *Blowiella* or *Leupoldina*) have been found yet in the North Sea wells studied, and no taxa which could be referred to the macroperforate and muricate Hedbergellidae have yet been found in beds as old as Barremian and Early Aptian.

The species of the Praehedbergellidae which have been identified have been used to define five informal Zones, which have been found to range in age from Early and Late Barremian to Early and Late Aptian. The Earliest Aptian may be recognised by the oldest stratigraphical occurrence of the genus *Lilliputianella*.

INTRODUCTION

Members of the Praehedbergellidae are microperforate globigerines with trochospiral tests (at least in their initial growth stage) and non-muricate and non-pustulate test walls. They range in age at least from Hauterivian to Danian and have been recorded from localities as far west as northern Mexico (Longoria, 1974), as far north as North Yorkshire, England (Banner and Desai, 1988), as far south as the Walvis Ridge, South Atlantic (Caron, 1985) and as far east as offshore Abu Dhabi (Banner and Strank, 1987). Species now assigned to genera of this family have been known since 1938 (*Globigerina* sp. D9, Hecht, 1938, now *Blefuscuiana aptiana* (Bartenstein)), and many (including *Gorbachikella kugleri* (*Bolli*); *Praehedbergella sigali* (Moullade); *B. occulta* (Longoria) and *Lilliputianella kuhryi* (Longoria)) have been used as zonal indices by previous workers (e.g. Bandy, 1967; Longoria, 1974; Sigal, 1977; Grigelis and Gorbachik, 1980; Gorbachik and Kuznetsova, 1983 and Banner and Desai, 1988).

The most comprehensive recent work on the Praehedbergellidae is that by Banner and Desai (1988) in their review and revision of the Jurassic–Early Cretaceous Globigerinina. These authors summarized the known stratigraphic ranges and phylogenetic affinities of all the contained genera of the Praehedbergellidae (three of the five of which were erected by them) as well as of some of the species. From this work it appears that some of the praehedbergellids may be usable for stratigraphic subdivision of part of the Early Cretaceous (Banner and Desai, 1988, fig. 1). The new data came, however, solely from Late Aptian assemblages of Speeton, north Yorkshire; none of the older Cretaceous beds at Speeton have been found to contain any planktonic foraminifera (it is probable that the Berriasian–Early Aptian deposits there were formed in water which was too shallow). Therefore, deeper-water deposits from the North Sea area were studied. Subseabed samples (cores and side-wall cores) from four wells, drilled (by BP Petroleum Development Ltd and Britoil plc) in the Cromer Knoll Group of the Central North Sea, were used. The correlation and dating of these sample-sequences had been determined by palynology and micropalaeontology, aided by lithostratigraphy and seismostratigraphy; the taxonomic determination of the praehedbergellid assemblages recorded here were, therefore, largely independent of any biostratigraphic conclusions which they may have suggested.

It is to be hoped that our results will help further our knowledge of the phylogeny of the Praehedbergellidae, and particularly aid in refining the planktonic foraminiferal biostratigraphy of deep-water sediments of Barremian to Aptian age.

PRACTICAL TAXONOMY AND BIOSTRATIGRAPHY

The generic characteristics recorded here (see below) can usually be readily distinguished by examination with an optical stereomicroscope, but we have found it to be essential to study these small praehedbergellids by SEM before final distinctions between members of the species-groups can be determined.

For the latter, we have used the methods of taxonomy employed by Banner and Desai (1988) and which have also been used for other very small globigerines (belonging to *Praetenuitella* Li Qianyu, *Tenuitella* Fleisher, and *Tenuitellinata* Li Qianyu) by Li Qianyu (1987). In particular, we have preferred to 'split' rather than to 'lump', while recognising that future studies may show at least some of our species or subspecies to be synonyms. It will be easier, in the future, to synonymise rather than to separate; it would be especially difficult to disentangle the biostratigraphic records of forms which would now be referred to separate taxa.

Criteria within the species-groups

We have used the following characters to distinguish between species or subspecies of similar test size:

(a) the height of coiling, number and shape of the chambers in each of the whorls, as seen dorsally;

(b) the rate of increase in chamber size with growth (either rapid or gradual);

(c) the degree of intercameral sutural depression at the periphery (measured here by the angle between the chambers, the 'intercameral angle of sutural depression', at the periphery);

(d) the size and relative depth of the umbilicus (the latter being determined primarily by the degree of overhang of the chambers of the last whorl; it may be shallow or deep);

(e) the number of chambers seen ventrally to actually abut the umbilicus in the last mature whorl;

(f) the shape of the aperture (e.g. slit-like or high-arched);

(g) the nature of the test-wall surface (whether or not there are perforation-cones).

Although most of the morphocharacters used can, with experience, be recognised by optical stereomicroscopy in well-preserved specimens, the perforation-cones (similar to those figured for *Blefuscuiana* by Banner and Desai, 1988, pl. 3, fig. 5b) may still be difficult to see optically. To overcome this practical difficulty we have defined the species *sensu lato* to encompass forms with and without perforation-cones (but otherwise morphologically identical) and regard the presence or absence of perforation cones as of subspecific importance. Groups which differ only in a single character (e.g. chamber height *or* the magnitude of the intercameral angle of sutural depression) are usually also given only subspecific status.

Criteria within the genus-group

The distinction between *Praehedbergella* and *Blefuscuiana*, applied by Banner and Desai (1988) needs modification in the light of new data presented here. Banner and Desai (1988) distinguished *Praehedbergella* from *Blefuscuiana* by the presence of 4–4½ rather than 5 or more chambers per whorl. Specimens with 6½ chambers in the penultimate whorl reducing to 4½ in the last whorl, however, also exist (e.g. Pl. 2, fig. 1c). Moreover, there are species in which the last whorl is clearly seen to be made of 5 chambers when viewed from the dorsal side, but only part of the fifth is seen ventrally; this may be visible at the periphery only (e.g. Pl. 2, fig. 4a–c), or it may extend into the umbilicus (e.g. Pl. 3, figs. 1a–c, 6a–c).

Any distinction based on the number of chambers in the final whorl is, of course, arbitrary. Nevertheless, since forms with only 4 chambers surrounding the umbilicus in the last whorl have been recorded from strata of Hauterivian (see *P. handousi* Salaj, 1984, figs. 2a–c) to Late Aptian (e.g. *P. grigelisi* Banner and Desai, 1988, pl. 2, figs. 8–13) age, while those with more than 4 such chambers are known to range from the Early Barremian (e.g. *B. laculata* n.sp. *s.s.*, Pl. 2, figs. 1–5) to the Early Danian (e.g. *B. archeocompressa* (Blow, 1979)), it is necessary to distinguish between these morphologies so that they may be used to biostratigraphic advantage.

In consequence, we redefine the genus *Praehedbergella* as containing individuals in which the umbilical limits are formed by 4 chambers only; part of a fifth chamber may be visible ventrally at the periphery, but this chamber does not extend into the umbilicus (e.g. *Praehedbergella pseudosigali* n.sp., Pl. 2, figs. 1a–c). In such forms, the dorsal (spiral) side may disclose that the last whorl is made of 5 chambers, as in some species of *Blefuscuiana* (e.g. *B. laculata s.s.*, Pl. 3, figs. 1a–c), but in the latter genus the 5 chambers of the last whorl, which are visible ventrally, all abut the umbilicus.

To assign specimens either to *Praehedbergella* or to *Blefuscuiana* without recognising any intermediate forms is, perhaps, misleading in that it suggests that the distinction between the two is discrete. This, in fact, is not the case and there are assemblages where the two intergrade (e.g. see *P. sigali s.s.* and *B. laculata s.s.* below); in other words, the evolution from *Praehedbergella* to *Blefuscuiana* illustrates 'phyletic gradualism'.

Biostratigraphy with morphological criteria

No Barremian or Early Aptian samples have been found (or are known to have been recorded) to contain muricate and macroperforate Hedbergellidae. Only the microperforate, non-muricate Praehedbergellidae, often with perforation-cones, are known from sediments of these ages.

It appears that the stratigraphically earliest specimens that may be assigned to *Praehedbergella* (e.g. those of *P. handousi* figured by Salaj, 1984, from the Early Hauterivian of Tunisia) had 4 chambers in each of the penultimate and the final whorls. By the Early Barremian, some (e.g. those of *P. sigali s.l.*, Pl. 2, figs. 2–3) had 4–4½ chambers in each of these whorls, while others (e.g. *P. pseudosigali* n.sp., Pl. 2, figs. 1a–c) had developed 6 chambers in the penultimate whorl, with almost 5 in the final whorl when seen dorsally, but only 4 abut the umbilicus ventrally.

The earliest known members of *Blefuscuiana* (Early Barremian) include forms with between 4 and 5 chambers abutting the umbilicus ventrally (e.g. *B. laculata s.l.*, Pl. 3, figs. 1–5 and *B. daminiae s.l.*, Pl. 3, figs. 6 and Pl. 4, figs. 1–3) as well as those with 5–6 such chambers (e.g. *B. aptiana* (Bartenstein), Pl. 7, figs. 1–4, and *B. praesimilis* n.sp., Pl. 8, figs. 4–6). Morphologically more advanced forms with 7 or 8 chambers in the final whorl are not known below the Late Aptian (e.g. *B. occulta* (Longoria, 1974), and *B. multicamerata* Banner and Desai, 1988). Since forms with 5 chambers in their last whorls occur through to the last occurrence of the genus (Early Danian) the 5–6 last-chambered forms are not separated generically from those with 7 and 8 such chambers. It is, however, worth noting that the latter have not yet been recorded in beds younger than the Early Albian.

Lilliputianella, with its later chambers higher than broad when seen dorsally, was not found below the Aptian at Speeton (Banner and Desai, 1988), and the earliest stratigraphical appearance of this praehedbergellid morphology appears to be in the earliest Aptian of the drilled sequences examined by us from the Central North Sea.

PREVIOUS WORK ON NORTH SEA BARREMIAN-APTIAN PRAEHEDBERGELLIDAE

Although outlines of the lithostratigraphy and micropalaeontology of Cretaceous of the North Sea Basins have been published (e.g. by King *et al.*, 1989), no detailed research on Barremian–Aptian planktonic foraminifera from the North Sea Basins has yet been publicly recorded. Several authors have described the broad succession of planktonic foraminiferal assemblages, but the work was done before the detailed revision of the genera and species from the Late Aptian of the area was published (Banner and Desai, 1988). Consequently, most of the taxa described in the present paper have been consistently referred to in print, collectively and incorrectly, as '*Hedbergella infracretacea*'. We include a revision of that taxon in this paper, and it can now be included among the many species referable to *Blefuscuiana*.

Ball (in Lott *et al.*, 1985) recorded and figured '*Hedbergella infracretacea*' from borehole 81/40 in the western margin of the Central North Sea Basin, and described a flood abundance of the species in a red mudstone clearly correlatable with the V5 Unit (*ewaldi* Marl) fauna described below in the present paper. The inadequacy of the figure and the lack of written description, however, prevents the allocation of Ball's specimens to particular taxa described in the present paper.

Crittenden (1987) discussed the Aptian planktonic foraminifera recovered from wells in Southern North Sea block 49. This essentially stratigraphical paper did not provide figures or descriptions of the globigerinid taxa. However, the paper did contain a general description of the succession of Aptian planktonic foraminiferal faunas which can be related to the Central North Sea sequence reported in this present paper. Crittenden (1987) reported the occurrence of '*Hedbergella aptiana*', with grey-coloured preservation, at the base of the Lower Holland Marl Member (although this taxon was shown by him to range higher, on his figure 4). This was recorded to be succeeded, in block 49, by a major flood of red-stained '*H. aptiana*' (referred to as red-stained '*H. infracretacea*' in the text of the paper) in the mid-part of the Lower Holland Marl. On gamma-ray and sonic logs, this unit seems similar to the V6 Unit of the Valhall Formation in the Central North Sea, and the contained microfauna very probably correlates directly with that given for Zone 4 in the present paper. At the top of the Lower Holland Marl Member, Crittenden (1987) recorded the presence of a green-stained assemblage referred to the '*H. infracretacea* group'; he believed this to be of Late Aptian age, on the basis of its content of the benthonic foraminifera *Saracenaria spinosa* Eichenberg and *Gaudryina dividens* Grabert, suggesting to Crittenden an equivalence with the *nolani-jacobi* Zones of the Northwest German Upper Aptian (Bartenstein and Kaever, 1978; King *et al.*, 1989). However, *G. dividens* has also been reported from beds of the Speeton Clay as old as Early Barremian (Lott *et al.*, 1985).

King *et al.* (1989) described from the Southern and Northern North Sea (i.e. south and north, respectively, of the Mid-North Sea High) a succession of planktonic foraminifera comparable to that given by Crittenden (1987). However, they described the three Aptian zones described by Crittenden (and as described here) to a single '*Hedbergella infracretacea*' Zone, called 'FCS7' in the Southern North Sea and 'FCN7' in the Northern North Sea. This 'zone' was referred to the Early Aptian–Late Aptian interval, and was said to comprise two planktonic foraminiferal events. The upper '*H. infracretacea*' occur in a calcereous claystone in which the calcareous microfossils exhibit a green, grey or grey-brown colour of preservation. Down section, red-stained '*H. infracretacea*' occur abundantly, originating from a red mudstone. These two 'events' clearly correspond to zones 4 and 5 of the present account.

Although King *et al.* (1989) also noted the presence of '*Hedbergella spp*' in the Mid Barremian *Gavelinella barremiana* Zone, none of the species or specimens were described in detail.

Crittenden *et al.* (1991) briefly recorded the occurrence of distinctive planktonic foraminiferal assemblages in the Lower Cretaceous of the Central North Sea. However, no taxonomic discussion or figures of the species were provided, as the paper was essentially lithostratigraphic — the only biostratigraphic information given was that needed to support the lithostratigraphy. The authors (Crittenden *et al.*, *op. cit.*) reported the development of three planktonic foraminiferal associations within the Aptian beds, comparable to those described by Crittenden (1987) from the Southern North Sea. An upper assemblage (comprising green-stained '*H. infracretacea*' and '*Globigerinelloides spp*') at the base of the Sola Formation was interpreted as being indicative of the Late Aptian *nutfieldensis* Zone transgression. This was followed down-section by a red-stained assemblage at the top of the Valhall Formation (V6 Unit), the characteristic species being referred to as '*Hedbergella* D11 Hecht, 1938'. This was interpreted as being earliest Late Aptian to latest Early Aptian in age. This contrasts with the age interpretation given by Crittenden (1987) as late Early Aptian for (probably) the same red-stained fauna occurring in the Southern North Sea block 49 wells. In the Central North Sea (Crittenden *et al.*, 1991), the lowest assemblage referred to the Aptian was that called '*Hedbergella* D9 Hecht, 1938' (= '*H. aptiana*' Bartenstein, also now referable to *Blefuscuiana* and discussed below in this paper); it occurred in the V5 Unit (Fischschiefer), and the specimens were often flattened, typically pyritised, with grey colour and black speckling. These 'events' clearly relate to zones 3, 4 and 5 of the present account (Fig. 4, p. 19).

From the Barremian, Crittenden *et al.* (1991) recorded the presence of '*Hedbergella spp*' in the Valhall Formation V4 Unit (said to be of 'Late to Middle Barremian' age). This assemblage probably corresponds to the Zone 2 association described in the present paper. No mention was made of planktonic foraminifera in the Lower Barremian of the Central North Sea, which is surprising as the Early Barremian fauna (Zone 1 herein) is widespread and distinctive — although it could be misinterpreted as a caved assemblage when found in cuttings samples.

Our biostratigraphic conclusions follow our account of the systematic descriptions and taxonomy of the species so far encountered, and are summarised in Fig. 4.

MATERIAL AND METHODS

This reconnaissance study is based on washed samples from the Cromer Knoll Group (basal Sola Formation and upper part of the Valhall Formation) drilled in three wells (15/30–3, 16/28–6RE and 20/2–2) of the Central North Sea area.

The subsurface samples were from cores, sidewall cores and cuttings, and the first two enabled errors of recorded distribution (caused by caving of specimens in the cuttings) to be avoided. The specimens were small but had to be picked and initially sorted optically; representatives of each sorted group were mounted on small pieces of photographic bromide paper for stereoscanning electron photomicrography; no liquid adhesives were used, so that the test-surfaces remained unaffected. Three views of each specimen (using contact prints from 35 mm negative film) were made to avoid errors of identification. It was found that the SEM imagery enabled recording of the significant morphology which could then be recognised using the optical microscope. The reverse procedure alone (i.e. using SEM imagery only as a final, illustrative, but not as an initial, research tool) was found to be prone to mistakes. Once the essential morphology of the taxa was understood, then their distribution in the wells was determined.

All holotypes, paratypes and hypotypes from the North Sea area, with the other specimens listed, are deposited in the Micropalaeontology collections, Department of Palaeontology, The Natural History Museum, London SW7 5BD, and all are registered with catalogue numbers prefixed 'P', as given in this paper. The specimens of *Blefuscuiana infracretacea s.s.* (= *Globigerina infracretacea* Glaessner) are two of the three specimens in the same slide (no. 689757) and are returned to the Department of Paleontology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA.

SYSTEMATIC PALAEONTOLOGY

All figured specimens, and many others which are referred to, are deposited in the Department of Palaeontology, The Natural History Museum, London. The depths given for the samples refer to those below the kelly bushing ('BKB') on the drilling rig, and, for accuracy and reliability of record, are given as they were initially and correctly recorded, i.e. in metres for the samples from Well 16/28–RE, and in feet for those from wells 20/2–2 and 15/30–3.

Superfamily GLOBIGERINACEA Carpenter, Parker and Jones, 1862
Family **PRAEHEDBERGELLIDAE** Banner and Desai, 1988
Genus **PRAEHEDBERGELLA** Gorbachik and Moullade, 1973

TYPE SPECIES. *Globigerina tuschepsensis* Antonova, 1964.

DIAGNOSIS EMENDED. Test a low trochospiral of 2 or more whorls, with 4–5 chambers visible in the dorsal aspect of the final whorl, but with only 4 chambers abutting the margins of the ventral umbilicus. The chambers are not radially elongate; the spiral side is evolute and the ventral side almost wholly involute. The aperture is intra-extraumbilical, interiomarginal, with a porticus; there are no accessory or supplementary apertures. The wall is calcitic, microperforate and lacks muricae or keels.

REMARKS. The need for this emendation is explained above (Practical Taxonomy and Stratigraphy; Criteria within the genus-group) in order more precisely to distinguish *Praehedbergella* from the longer-ranging genus *Blefuscuiana*.

Praehedbergella grigelisi Banner & Desai ***perforare*** n. ssp. Pl. 1, figs. 1a–d

NAME. After *perforare*, to pierce through, referring to the presence of perforation cones.

DIAGNOSIS. Characterized by the presence of perforation cones, the low trochospire, the relatively few chambers (about 5) in the first whorl, rapid opening of the spire and apparently narrow slit-like aperture.

PROVENANCE OF TYPES.
Holotype. P52758, from North Sea Well 20/2–2, 8300 m, Earliest Aptian; Pl. 1, figs. 1a–d.
Paratypes. From North Sea Well 16/28–6RE; P52759 (4275 m), P52762 (4204 m) (both Early Barremian), P52760 (4000 m), P52761 (4075 m) (both Late Aptian).

DESCRIPTION. Adult test about 0.20 mm at its maximum diameter and comprises at least two whorls of chambers coiled in a low trochospire. There are about 5 chambers in the penultimate whorl, reducing to 4 or 4½ chambers in the last whorl. The spiral side is almost flat or slightly convex and the intercameral sutures are moderately depressed; the intercameral angle of sutural depression at the periphery is about 135°. The chambers themselves are symmetrical and increase significantly in size with growth, those (excluding the final chamber) in the last whorl become slightly depressed, being about 2/3 as high as long when viewed from the spiral side. The final chamber may be only slightly longer than high. The umbilicus is shallow and measures about 0.35 mm in diameter. The aperture appears to be a narrow slit and perforation cones are visible at least on chambers of the last whorl.

REMARKS. The presence of perforation cones in this subspecies is of particular interest since these have not previously been recorded for any member of this genus. In the related genus *Blefuscuiana*, forms exist with identical gross morphologies which may be distinguished only by the presence or absence of perforation cones (e.g. *B. aptica* (Agalarova) *sensu stricto*, *B. infracretacea* (Glaessner) (metatypes redescribed in this paper) and its perforation-cone-bearing equivalents called 'cf. *aptica*' by Gorbachik, 1986, and by Banner & Desai, 1988). Since several such pairs are known for this genus (see below) we now regard the presence or absence of perforation cones as being only of subspecific value. Similarly, in *Praehedbergella*, we use perforation-cones to distinguish subspecies when the gross morphology of the taxa is otherwise identical.

Although *P. grigelisi perforare* resembles in all but generic characters the juvenile form of *B. aptica depressa*, the two do not occur consistently together and we regard them here as taxonomically separate.

P. grigelisi is *nomen correctum* for *P. grigelisae* Banner & Desai, 1988.

DISTRIBUTION. Central North Sea: Well 16/28–6RE

(4000 m, 4075 m, 4204 m and 4275 m); Well 20/2–2 (8300 m).

STRATIGRAPHY. Early Barremian to Late Aptian.

Praehedbergella pseudosigali n.sp. Pl. 2, figs. 1a–c

NAME. After superficial similarity of this species to *P. sigali*.

DIAGNOSIS. Characterized by the presence of perforation cones, low trochospire, relatively large number of chambers (about 6½) in the penultimate whorl, gradual opening of the spire and high-arched aperture.

PROVENANCE OF TYPE.
Holotype. P52735, Pl. 2, figs 1a–c. From Central North Sea Well 20/2–2, Late Barremian (8370 m).

DESCRIPTION. Test about 0.25 mm at its maximum diameter, consisting of two whorls of chambers coiled in a low trochospire. There are about 6½ chambers in the penultimate and 4½ in the last whorl. The spiral side is only slightly convex, with intercameral sutures forming intercameral angle of sutural depression at the periphery of about 145°. The chambers themselves are symmetrical and increase in size gradually with growth, those (excluding the final chamber) in the last whorl become depressed, being about half as high as long (compared with about 2/3 as high as long in the final chamber) on the spiral side. The umbilicus is small and the aperture is a high arch, with a very narrow porticus. Perforation cones are visible on chambers of the last whorl.

REMARKS. The presence of perforation cones, the numerous (about 6½) chambers in the first whorl, and the high-arched aperture is sufficient to describe this as a new species, and in particular to distinguish it from *P. sigali* (Moullade) *sensu lato*.

DISTRIBUTION. Central North Sea (Well 20/2–2, 8370 m).

STRATIGRAPHY. Late Barremian.

Praehedbergella ruka n.sp. *sensu lato*. Pl. 1, figs. 2a–c, 3a–c, 4a–b, 5a–c.

NAME. After the Norwegian *ruka*, meaning a heap, stack or pile, referring to the 'heap' of chambers forming the high spire and very convex dorsal surface.

DIAGNOSIS. Characterized by its high trochospire, strong dorsal convexity (and 4 to 4½ chambers in the last whorl).

DESCRIPTION. Test about 0.15 mm at its maximum diameter, comprising about three whorls coiled in a high trochospire. There are 5 chambers in the penultimate whorl but 4–4½ in the final whorl. The spiral side is strongly convex and the intercameral sutures are moderately depressed forming intercameral angles of about 135°–140° at the periphery of the test. The chambers are symmetrical and increase in size gradually with growth. The chambers in the last whorl are either slightly depressed (about 2/3 as high as long when viewed from the spiral side), or depressed (about half as high as long when viewed dorsally). The final chamber may be about as high as long. The umbilicus is small and the aperture is a narrow slit.

REMARKS. This species of *Praehedbergella* has a dorsal convexity greater than that of any other known species of the genus, but which is matched only by a new species of *Blefuscuiana* (*B. cumulus*) described below.

STRATIGRAPHY. Aptian.

Praehedbergella ruka n.sp. *sensu stricto* Pl. 1, figs. 2a–c

DIAGNOSIS. Characterized by its high trochospire, strong dorsal convexity, slightly depressed chambers (about 2/3 as high as long) in the last whorl (excluding the final chamber which may be subglobular), and a smooth test surface lacking perforation cones.

PROVENANCE OF TYPES.
Holotype. P52739, Pl. 1, figs. 2a–c; from Central North Sea Well 16/28–6RE, Early Aptian (4157.5 m).
Paratypes. P52740, P52741, both from Well 16/28-6RE, Early Aptian (4150.5 m).

REMARKS. *P. ruka ruka* is distinguished from the other *ruka* subspecies by having only slightly depressed chambers and by lacking perforation cones.

DISTRIBUTION. Central North Sea.

STRATIGRAPHY. Early Aptian.

Praehedbergella ruka contritus n.sp., n.subsp.
Pl. 1, figs. 3a–c, 4a–b

1978 *Hedbergella infracretacea gargasiana* (Moullade), Caron: 652–656, 658; Pl. 1, figs. 7–9 (*not Globigerina infracretacea* Glaessner subsp. *gargasiana* Moullade, 1961).
1982 ?*Hedbergella hoterivica* (Subbotina), Crittenden: 30–31, Pl. 2, figs. 1–2.

NAME. After *contritus*, a worn down object, referring to the depressed chambers in the last whorl.

DIAGNOSIS. Characterized by its high trochospire, strong dorsal convexity, depressed chambers (excluding the last) in the final whorl (about half as high as long when viewed spirally), and a smooth test surface lacking perforation cones. The final chamber may be subglobular.

PROVENANCE OR TYPES.
Holotype. P52737, Pl. 1, figs. 3a–c; from Central North Sea Well 16/28–6RE, Late Aptian (3989.5 m).
Paratype. P52738, Pl. 1, figs. 4a–b; from Central North Sea Well 20/2–2, Early Aptian (8250 ft).

REMARKS. The specimens of *P. ruka* figured by Caron (1978) came from beds she believed to be upper Aptian and which were in the lowest core obtained from DSDP Site 364, Angola Basin; unfortunately, she misidentified it as '*Hedbergella infracretacea gargasiana* Moullade', a form which has 5½ high, undepressed chambers in the final whorl, and which is referable either to *Blefuscuiana* or to *Hedbergella* (with a muricate test surface). The only resemblance between *P. ruka* and Moullade's form is the great convexity of the dorsal side. The holotype of *P. ruka contritus* occurred in the Upper Aptian but it may be reworked there; we have not seen evidence for its occurrence in beds of Late Aptian age elsewhere. We suspect that the earliest cores retrieved from DSDP Site 364 were, in fact, of Early Aptian age.

A similar form has been figured by Crittenden (1982) from the Atherfield Clay (Early Aptian) of the Isle of Wight, southern England. He called it '*Hedbergella hoterivica*', but that species belongs to the genus *Favusella* (Banner & Desai, 1988); Crittenden's specimens posses a high spire and dorsal convexity, and lack perforation-cones, but their re-examination is necessary before identity with this subspecies is confirmed.

DISTRIBUTION. Angola Basin and Walvis Ridge, southeastern Atlantic Ocean; Central North Sea; ?southern England.

STRATIGRAPHY. Early–?Late Aptian.

Praehedbergella ruka papillata n.sp., n.ssp.

Pl. 1, figs. 5a–c

NAME. After *papillatus*, with buds (referring to the presence of abundant perforation cones).

DIAGNOSIS. Characterized by its high trochospire, strong dorsal convexity, depressed chambers (excluding the last) in the final whorl, a papillate test surface, covered with abundant perforation cones, and a thick porticus. The final chamber may be subglobular.

PROVENANCE OF TYPES

Holotype. P52736; Pl. 1, figs. 5a–c, from Central North Sea (Well 16/28–6RE), 4150 m, Early Aptian.

REMARKS. This subspecies appears not to have been recognised by any previous workers. Although it is distinguished by the presence of its perforation cones, it can be morphologically otherwise identical to the typical form of the species (see Pl. 1, compare figs. 5c and 3c). *P. ruka papillata* appears to be analogous to *Guembelitria cretacea* Cushman, which also has perforation cones formed over its microperforations, while *P. ruka ruka* would be analogous to *Gallitellia vivans* (Cushman), which has a smooth microperforate surface (see Loeblich and Tappan, 1988, Pl. 485, figs. 1–3, 11–12); such distinctions were used by Loeblich and Tappan (1988, p. 453) to distinguish between the genera *Guembelitria* and *Gallitellia*. However, we use this criterion to distinguish only subspecies (not even species, much less genera) because we, as yet, do not know of any stratigraphic difference between the geological ranges of these taxa (in contrast, *Guembelitria* ranges Cretaceous–Palaeogene, while *Gallitellia* is Quaternary). However, the geographical distribution of the subspecies may prove to be different.

The thick, broad, heavy porticus, which appears to characterise *P. ruka papillata* (Pl. 1, fig. 5a) is apparently not typical for other taxa which bear perforation cones, either in the Globigerinacea (e.g. *P. grigelisi perforare*, Pl. 1, fig. 1a, and *Blefuscuiana infracretacea* (Glaessner), Pl. 4, fig. 2, Pl. 8, fig. 1) or the Heterohelicacea (e.g. *Cassigerinella boudecensis* Pokorny, see Li Qianyu, 1986).

DISTRIBUTION. Central North Sea.

STRATIGRAPHY. Early Aptian.

Praehedbergella sigali (Moullade) *sensu lato*.

Pl. 2, figs. 2a–c, 2a–c

1966 *Hedbergella* (*Hedbergella*) *sigali* Moullade; 87–88: Pl. 7, figs. 20–25.

DIAGNOSIS EMENDED. A species of *Praehedbergella* in which the number of chambers in each of the penultimate and last whorls is 4 to 4½, the chambers are anteriorly-posteriorly symmetrical (the highest part of each chamber being in the middle of its length), and the aperture is narrow. The intercameral sutures form intercameral depressions at the periphery of about 125° to about 140°. Perforation cones have never been recorded in this species.

REMARKS. The aperture is a narrow slit, not a broad arch as it is in *P. pseudosigali*. The spiral side is not strongly convex as it is in *P. ruka*. The chambers of the last whorl are symmetrical, their greatest height being at the mid point of their length; this differs from the asymmetrical chambers figured by Gorbachik (1986) for topotypic *P. tuschepsensis*.

The chambers of the last whorl vary in height from being subglobular to weakly depressed; the holotype microphotographed by Moullade (1966, Pl. 7, figs. 24–25) has subglobular chambers, of height almost as great as their length (when viewed from the spiral side), and correspondingly deep intercameral sutures at the test periphery (which make angles of about 125–130° between the chambers). This form is regarded here as *H. sigali sensu stricto* (i.e. *H. sigali sigali*, see below). In contrast, other forms of this species have depressed chambers, which have heights about half their lengths (when viewed from the spiral side), in their final whorls; these latter are separated by us as two new subspecies (*compacta* n.subsp. and *rasilis* n.subsp., see below) distinguished by the magnitude of their peripheral intercameral angles and overall appearance of their tests.

STRATIGRAPHY. Early Barremian–Late Aptian (see subspecies below).

Praehedbergella sigali (Moullade) *sensu stricto*

Pl. 2, figs. 2a–c

1966 *Hedbergella (Hedbergella) sigali* Moullade: 87–88, *pars*; Pl. 7, figs. 21, 24–25 (*non* 20, 22, 23).

1985 *Hedbergella sigali* Moullade, Caron: 59; fig. 25 (22a–b, *non* 21a–c).

Non *Hedbergella sigali* Moullade, Kuhry, 1974, p. 231, Pl. 2, figs. 6a–c, 8.

Non *Hedbergella sigali* Moullade, Longoria, 1974, p. 68, Pl. 21, figs. 6–8, Pl. 22, 1–13.

REMARKS. Moullade (1966) erected *Hedbergella sigali* and distinguished it from *H. delrioensis* by its smaller, less coarsely perforate test with a less rugose surface. These criteria, together with the Early Barremian–Early aptian range of the species, later led Banner and Desai (1988) to suggest that '*Hedbergella*' *sigali* should be referred to *Praehedbergella*. Although it is acknowledged that further work on the primary types or topotypes is needed before this can be made certain, the view taken by Banner and Desai (op. cit.) is adopted here.

Kuhry (1974) assigned specimens from S.E. Spain with 4–5 chambers in the last whorl to '*Hedbergella*' *sigali*, but only figured individuals with 5 and 6 such chambers. Consequently Kuhry's specimens are better assigned to *Blefuscuiana* and are not included here in the synonymy of *P. sigali*. Similarly, specimens figured by Longoria (1974), in which the chambers are distinctly longer than high, are not regarded as conspecific with *P. sigali*. Some of these (1974, Pl. 22, figs. 1–5) have been referred to *P. tatianae* Banner and Desai (1988), others (1974, Pl. 22, figs. 9–13) are referable to *Blefuscuiana*; the remaining specimen is deformed and indeterminate.

PROVENANCE OF HYPOTYPES. P52742 (Pl. 2, fig. 2), P52743, both North Sea Well 20/2–2, 8680 ft, Early Barremian; P52744 (4150.5 m, Early Aptian), P52745 (4010 m. Late Aptian), both North Sea Well 16/28–6RE.

DISTRIBUTION. Central North Sea; Hautes-Alpes, southeastern France.

STRATIGRAPHY. Moullade (1966) reported *H. sigali* (including forms assigned here to *H. sigali rasilis* n.ssp.) as ranging from the Early Barremian–Early Aptian and this range is also recorded here for typical forms of this species. However, a single occurrence was also observed in the Late Aptian of Well 16/28–6RE (at 4010 m); this may be a true range extension but it may be a record of a reworked specimen (the sample originates from within a basin fan facies).

Praehedbergella sigali (Moullade) ***compacta*** n. ssp.

Pl. 2, figs. 3a–c

1966 *Hedbergella* (*Hedbergella*) *sigali* Moullade: 87–88 *pars*; Pl. 7, fig. 20.

NAME. After the more 'compact' outline of the test compared with *P. sigali sigali*.

DIAGNOSIS. A subspecies of *P. sigali* (Moullade) *sensu lato*, characterized by chambers which (sometimes excluding the final chamber) become depressed in the last whorl and have heights about half their lengths (when viewed from the spiral side), by relatively shallow intercameral sutures, which form intercameral angles of about 150° at the test periphery, and by a 'compact' test outline.

PROVENANCE OF TYPES.
Holotype. P52746 (Pl. 2, figs. 3a–c), from Central North Sea Well 20/2–2, 8680 ft (Early Barremian).
Paratypes. All from Central North Sea Well 16/28-6RE; P52753 (4189 m), P52752 (4204 m), P52756 (4225 m), all Early Barremian; P52748–P52751, P52754, P52755, P52757, all 4150.5 m, all Early Aptian.

DESCRIPTION. Test about 0.10–0.15 mm at its maximum diameter, comprising about two whorls, each with 4½ chambers coiled in a low trochospire. The spiral side is almost flat or slightly convex. The depressions of intercameral sutures at the periphery of the test form angles of about 150° between adjacent chambers. The chambers themselves are symmetrical and increase in size gradually with growth and become depressed, being almost half as high as long when viewed on the spiral side (excluding the final chamber); the final chamber is only slightly lower than long. The umbilicus measures about 0.02 mm in diameter, and the aperture is a narrow slit with a narrow porticus. Perforation cones are not present.

REMARKS. The 'compact' test outline in this species is apparently a consequence of the depressed chambers combined with the relatively shallow intercameral sutural depressions at its periphery.

A specimen figured by Moullade (1966, Pl. 7, fig. 20) resembles this species but has been photographed at a slightly oblique angle and should, therefore, only tentatively be included here in synonymy.

DISTRIBUTION. Central North Sea (Well 16/28–6RE, 4150.5 m, 4160.7 m, 4200 m; Well 20/2–2, 8680 m); ?Hautes-Alpes, southeastern France.

STRATIGRAPHY. Early Barremian–Early Aptian.

Praehedbergella sigali (Moullade) ***rasilis*** n. ssp.

1966 *Hedbergella* (*Hedbergella*) *sigali* Moullade: 87–88 *pars*; Pl. 7, figs. 22–23.
1985 ?*Hedbergella sigali* Moullade, Caron: 59 *pars*; figs. 25 (21a–c).
1986 *Clavihedbergella sigali* (Moullade), Gorbachik: 236; Pl. 24, figs. 1–2.

NAME. From Latin, *rasilis*, 'scraped, shaved, smoothed, polished', referring to the more rounded appearance of the test compared with *P. sigali sigali*.

DIAGNOSIS. A subspecies of *P. sigali sensu lato* characterized by its depressed chambers in the last whorl, which are about half as high as long, moderately depressed intercameral sutures, which form intercameral angles of about 140° at the periphery of the test, and a moderately lobate test outline (compared to the strongly lobate test of *P. sigali sigali*).

PROVENANCE OF TYPE.
Holotype. specimen figured by Gorbachik, 1986, Pl. 24, fig. 1, from Katsa, Verkhoretse, southwestern Crimea, U.S.S.R.; Late Barremian.

DESCRIPTION. Test about 0.20 mm at its maximum diameter, composed of about 2 whorls, coiled in a low trochospire, each with about 4½ chambers. Spiral side almost flat or slightly convex. Intercameral sutures forming angles of about 140° between chambers at the periphery of the test. The chambers are symmetrical and increase in size gradually with growth and become depressed, being almost half as high as long when viewed from the spiral side, in the last whorl. The aperture is a narrow slit bordered by a narrow porticus. The test surface lacks perforation cones.

REMARKS. The only published specimens definitely assigned to this species are those recorded by Moullade (1966) and Gorbachik (1986). The specimen figured by Caron (1985) is morphologically very similar, but it has not been described, the nature of its wall is obscure, and its stratigraphic primary provenance is uncertain (it was not mentioned by Caron, 1978, but she thought it to have come "from lower Aptian levels reworked in Albian sample" when she later figured it in 1985).

This subspecies has not so far been recorded from the North Sea.

DISTRIBUTION. Southern U.S.S.R.; Hautes-Alpes, southeastern France; ?Walvis Ridge, South Atlantic Ocean.

STRATIGRAPHY. Recorded as ranging from Early Barremian–Early Aptian, i.e. the same range as recorded by Moullade (1966) for *Praehedbergella sigali s.s.*.

Praehedbergella tuschepsensis (Antonova)

Pl. 2, figs. 4a–c

1964 *Globigerina tuschepsensis* Antonova: 59–60; pl.'12, fig.'3a–c.
1986 *Clavihedbergella tuschepsensis* (Antonova), Gorbachik: 118–9, 236; Pl. 25, fig. 1.

REMARKS. When Antonova (1964) erected *Globigerina tuschepsensis*, she published only drawings of her new species. Later, Gorbachik (1986) used scanning electron micrographs to illustrate a topotypic specimen (1986) with clearly asymmetric chambers (with greatest height about two-thirds of their length towards the posterior). This character is exhibited by the North Sea specimens and is unknown in any other species of this genus.

PROVENANCE OF HYPOTYPES. P52733 (Pl. 2, fig. 4), from central North Sea Well 16/28–6RE, 4150.5 m, Early Aptian.

DISTRIBUTION. Central North Sea (Well 16/28–6RE, 4150.5 m to 4250 m); Southern U.S.S.R.

STRATIGRAPHY. Recorded from the Barremian to Early Aptian of the southern U.S.S.R. (Antonova, 1964 and Gorbachik, 1986) and from the Early Barremian to Early Aptian of the Central North Sea.

Praehedbergella sp. cf. ***P. handousi*** (Salaj, 1984)
Pl. 2, figs. 5a–c

REMARKS. The specimens assigned here resemble '*Caucasella*' *handousi*, a species erected by Salaj (1984, from the Early Hauterivian of Tunisia) but are smaller (0.12 mm in maximum diameter, compared with 0.3 mm for the type specimens of the species). Moreover, the initial chambers in the North Sea specimens are not clearly seen.

PROVENANCE OF HYPOTYPE. P52734, from Central North Sea Well 20/2–2, 8680 ft, Barremian.

Genus **BLEFUSCUIANA** Banner & Desai, 1988

TYPE SPECIES. *Blefuscuiana kuznetsovae* Banner & Desai, 1988.

DIAGNOSIS EMENDED. A Praehedbergellid as originally diagnosed, and which has 5 or more chambers abutting the umbilicus. The trochospiral test may have perforation-cones or a porticus or both, but it is always irregularly microperforate, not regularly macroperforate, and it lacks muricae.

REMARKS. The diagnosis has had to be emended in order more clearly and precisely to distinguish this taxon from *Praehedbergella* Gorbachik and Moullade. The adult chambers of both *Praehedbergella* and *Blefuscuiana* are no higher than long when seen dorsally, and have rounded, low peripheries; in contrast, *Lilliputianella* Banner and Desai has chambers which are higher than long when seen dorsally, and which develop narrowly elongate, sometimes even radially pointed, peripheries.

Blefuscuiana aptiana (Bartenstein, 1965) *sensu lato*
Pl. 6, figs. 4a–b, 5, 6a–b, 7; Pl. 7, figs. 1a–c, 2a–c, 3a–c, 4a–c.

REMARKS. When erecting this species, Bartenstein (1965) cited Hecht's (1938) figured specimens as the type series. Later, Banner and Desai (1988) pointed out that the holotype of *B. aptiana* (Hecht's Pl. 23, fig. 60; Bartenstein's text-fig. 3) appears to be deformed or abnormal and they used the paratypes for identification of the species. Although Bartenstein (1965) figured only drawings, it is apparent that these type specimens each comprise about 2 whorls coiled in a low trochospire, and have flat spiral sides; they have 5–6 chambers in their last whorls and intercameral sutural angles of about 120°–130° at the periphery of their tests. Their chambers are only slightly depressed (i.e. 2/3 or more as high as long when viewed spirally) and their test surfaces appear to be completely smooth, without perforation cones. These specimens are taken here to be typical of *B. aptiana* (i.e. of *B. aptiana s.s.*). Other morphologies which differ only in having more depressed chambers and/or possess perforation cones, however, are also included by us in the species *sensu lato* but are separated at subspecific level (see *B. aptiana depressa, B. aptiana implana* below).

STRATIGRAPHY. Barremian–Late Aptian (see subspecies below). The species has previously been recorded from the Southern North Sea (Crittenden, 1987, from block 49) and the Central North Sea (Crittenden *et al.*, 1991); these records were from beds of the basal Aptian (basal Lower Holland Marl Member and in the V5 Unit respectively). The basal Aptian acme of this species is widespread in the North Sea area, and this is seen here in the sample from 8300 ft depth, well 20/2–2, where it has a characteristic grey colouration with black speckles, originating from the pyritic and organic-rich sediments of the V5 Unit (Fischschiefer Member). This correlates with the characteristics of the same unit in north-west Germany, at which level the species was recorded by Hecht (1938) (see *B. aptiana sensu stricto*). Specimens from this horizon are commonly pyritised to varying degrees, due to the anoxicity of the bottom waters of this time (conditions represented by the Fischschiefer Member).

Blefuscuiana aptiana (Bartenstein) *sensu stricto*
Pl. 6, figs. 4a–b, 5, 6a–b

1938 ?*Globigerina* sp. D9 Hecht: 17; Pl. 23, fig. 60.
1938 *Globigerina* sp. D9 Hecht: 17; Pl. 23, figs. 61–63.
1965 *Hedbergella aptiana* Bartenstein: 347–348, text-figs. 3?, 4–6.
1979 *Hedbergella aptiana* Bartenstein; Sigal: 318; Pl. 2, figs. 24, 25.
1988 *Blefuscuiana aptiana* (Bartenstein); Banner & Desai: 158, figs. 1–3.
1988 *Blefuscuiana occulta* (Longoria) *quinquecamerata* Banner & Desai: 162–163; Pl. 7, figs. 9–11.

REMARKS. This species is characterised by having a relatively flat spiral side, an open umbilicus, which the chambers of the last whorl do not overhang significantly, 5–6 chambers in the last whorl, only slightly depressed chambers (about 2/3 as high as long when viewed dorsally) in the last whorl, and by the absence of perforation cones.

PROVENANCE OF HYPOTYPES. P52665 (Pl. 6, fig. 6), P52667 (Pl. 6, fig. 5), P52672, all from the Early Aptian, North Sea Well 16/28–6RE, 4178.5 m. P52675, from the Early Barremian, North Sea Well 20/2–2, 8600 ft. P52669, Well 16/28–6RE, 4100 m, Late Aptian. P52670, Well 16/28–6RE, 4150.5 m, Early Aptian. P52671, Well 16/28–6RE, 4160.7 m, Early Aptian. P52666 (Pl. 6, fig. 4), North Sea Well 20/2–2, 8300 ft, Early Aptian. P52668, Well 16/28–6RE, 4075 m, Late Aptian. P52673, Well 20/2–2, 8210 ft, Late Aptian. P52674, Well 20/2–2, 8300 ft, Early Aptian. P52676, Well 15/30–3, 12830–12840 m, Early Aptian.

DISTRIBUTION. Central North Sea (Wells); North-West Germany; Vigo Seamount, 200 kms offshore from Portugal (west of Oporto).

STRATIGRAPHY. Previously recorded from the Early to Late Aptian of Europe, the typical form of this species is now recorded from the Early Barremian to the Late Aptian of the North Sea.

Blefuscuiana aptiana (Bartenstein) ***depressa*** n.subsp.
Pl. 6, fig. 7; pl. 7, figs. 1a–c

NAME. After the depressed form of the chambers in the last whorl.

DIAGNOSIS. A subspecies of *B. aptiana* characterised by having depressed chambers (about half as high as long when viewed from the spiral side), and by lacking perforation cones.

PROVENANCE OF TYPES.
Holotype. P52711, Pl. 7, figs. 1a–c; from North Sea Well 16/28–6RE, 4260 m, Early Barremian.
Paratype. P52712, Pl. 6, fig. 7; from North Sea Well 20/2–2, 8300 ft, Early Aptian.

DESCRIPTION. Test about 0.15–0.2 mm at its maximum diameter, comprising about 2–3 whorls coiled in a low trochospire, each with 5–5½ chambers. The spiral side is almost flat or slightly convex and the intercameral sutures are moderately depressed, forming angles of about 130°–135° at the periphery of the test. The chambers are symmetrical and increase in size gradually with growth, becoming depressed in the second and (when present) third whorl, being about half as high as long when viewed dorsally. The last chamber may be about as high as long. The umbilicus is 'open' and the aperture appears to be a narrow slit. The test surface lacks perforation cones.

REMARKS. The depressed chambers in the last whorl of this species, combined with the absence of perforation cones distinguishes this subspecies from others of *B. aptiana*.

DISTRIBUTION. Central North Sea (Wells).

STRATIGRAPHY. Early Barremian–earliest Aptian.

Blefuscuiana aptiana (Bartenstein) ***implana*** n.subsp.
Pl. 7, figs. 2a–c, 3a–c, 4a–c

NAME. After *implanus*, uneven, referring to the rough surface of the test resulting from the presence of perforation cones.

DIAGNOSIS. A subspecies of *B. aptiana* characterised by having perforation cones.

PROVENANCE OF TYPES.
Holotype. P52705, Pl. 7, figs. 2a–c; from North Sea Well 20/2–2, 8210 ft, Early Aptian.
Paratypes. P52706, Pl. 7, figs. 4a–c; from Well 20/2–2, 8210 ft, Late Aptian. P52707, Pl. 7, figs. 2a–c; from Well 20/2–2, 8370 ft, Late Barremian.

DESCRIPTION. Test about 0.15–0.2 mm at its maximum diameter, comprising about 2–3 whorls coiled in a low trochospire. There are 5–6 chambers in each of the penultimate and last whorls. The spiral side is almost flat or slightly convex and the intercameral sutures are moderately depressed, forming angles of about 130°–140° at the periphery of the test. The chambers are symmetrical and increase in size gradually with growth, they are typically subglobular to slightly depressed (about 2/3 as high as long when viewed from the spiral side) in the last whorl, although in some the first 1–2 chambers in the last whorl may be more strongly depressed (about half as high as long). The umbilicus is broadly open and the aperture is a narrow slit. Perforation cones are present on chambers of the last whorl.

REMARKS. This subspecies differs from others of *aptiana* in having perforation cones.

DISTRIBUTION. Central North Sea (Well).

STRATIGRAPHY. Late Barremian–Late Aptian.

Blefuscuiana daminiae n.sp.
Pl. 3, figs. 6a–c; Pl. 4, figs. 1a–b, 3a–c

NAME. After Damini Desai, who took some initial SEM photographs and helped begin this phase of the study.

DIAGNOSIS. Characterised by having 5 chambers in the last whorl of which only part of the first is seen ventrally, thereby giving an overall subquadrangular appearance to the test and by a deep umbilicus, resulting from the distinct overhang of the chambers in the last whorl.

PROVENANCE OF TYPES.
Holotype. P52696 (Pl. 3, figs. 6a–c), from North Sea Well 15/30–3, 12830–12840 ft, Early Aptian.
Paratypes. P52699 (Pl. 4, fig. 3), from same sample as holotype. P52697, from North Sea Well 16/28–6RE, 4150.5 m, Early Aptian. P52698 and P52700, both from North Sea Well 20/2–2, Early Aptian, from 8300 ft (Pl. 4, figs. 1a–c) and 8250 ft respectively.

DESCRIPTION. Adult test about 0.20 mm at its maximum diameter, comprising at least 2 whorls coiled in a low trochospire. There are 5 chambers in each of the penultimate and last whorls. The spiral side is slightly concave to slightly convex and the intercameral sutures are moderately depressed, forming intercameral angles of about 140°–150° at the periphery of the test. The chambers are symmetrical and increase gradually in size with growth. They are subglobular in the penultimate whorl and depressed to slightly depressed (about 1/2–2/3 as high as long, when viewed from the spiral side) in the last turn of the spire, with the first two chambers in the latter tending to be more depressed than the last three. The final chamber may be almost as high as long. The umbilicus is small and deep; the aperture appears to be a narrow slit.

REMARKS. This species most closely resembles *B. infracretacea aptica* but differs in having only part of the first chamber in the last whorl visible ventrally. *B. daminiae* therefore appears to be morphologically less evolved than *B. infracretacea aptica*. Since *B. daminiae* is known only from the Early Aptian, while *B. infracretacea aptica* has been found in beds of Early to Late Aptian age (see below) it seems possible that *B. daminiae* may be the ancestral form.

The much more rapid chamber enlargement in the last whorl of this species, as seen dorsally, easily distinguishes it from *B. laculata s.l.*.

Although the holotype lacks perforation-cones and possesses a smooth surface, perforation-cones may be present on some specimens (e.g. Pl. 4, fig. 3a); these may merit subspecific distinction, but further study has yet to be made.

DISTRIBUTION. Central North Sea (wells).

STRATIGRAPHY. Early Aptian.

Blefuscuiana excelsa (Longoria) *sensu lato*

1974 *Hedbergella excelsa* Longoria: 55, 56; pl. 18, figs. 6–11, 14–16.

REMARKS. This is the only publicly described species of *Blefuscuiana* which has a high spire and a very convex dorsal surface. Specimens exactly matching the described type specimens, which must represent the typical form of the species *sensu stricto*, are not as yet known from the North Sea area; those which have been found are referred to the new subspecies, described below.

Blefuscuiana excelsa (Longoria) *cumulus* n.subsp.
Pl. 6, figs. 1a–c, 2a–c

NAME. From *cumulus* meaning a heap or pile, referring to the chambers forming the high spire.

DIAGNOSIS. Characterised by its high spired test, with its very convex dorsal surface, and by having 5 chambers in the last whorl.

PROVENANCE OF TYPES.
Holotype. P52708, Pl. 6, fig. 1a–c; from North Sea Well 15/30–3, 12830–12840 m, Early Aptian.
Paratypes. P52709 (Pl. 6, figs. 2a–c), P52710, both from North Sea Well 16/28–6RE, 4150.5 m, Early Aptian.

DESCRIPTION. Test about 0.20 mm at its maximum diameter, comprising about 2–3 whorls coiled in high trochospire. There are about 5 chambers in each of the penultimate and last whorls. The spiral side is strongly convex, and the intercameral sutures are moderately depressed, forming angles of about 135°–140° at the periphery of the test. The chambers are symetrical and increase in size gradually with growth, becoming depressed, being about half as high as long in the last whorl (when viewed from the spiral side). The umbilicus is small and deep, and the aperture is probably a narrow slit. Perforation-cones have not been found on this species.

REMARKS. *B. excelsa cumulus* differs from *B. excelsa* (Longoria) *sensu stricto* by its fewer chambers per whorl — the latter has at least six. *B. excelsa s.s.* has been recorded only from the Early Aptian; *B. excelsa cumulus* is also known in this study, only from the Early Aptian of the North Sea area.

DISTRIBUTION. Central North Sea (Wells).

STRATIGRAPHY. Early Aptian.

Blefuscuiana gorbachikae (Longoria). Pl. 6, figs. 3a–c

1974 *Hedbergella gorbachikae* Longoria: 56–58; pl. 15, figs. 1–16.
1985 *Hedbergella gorbachikae* Longoria; Caron: 1985: 31, 59; figs. 25.8–9.
1988 *Blefuscuiana gorbachikae* (Longoria); Banner & Desai: 160, 162; pl. 5, figs. 8–12 (including synonymy).

REMARKS. This species is characterised by its flat dorsal side, convex ventral side and strongly umbilically directed last chambers.

PROVENANCE OF TYPES. Early Aptian, P52687 (Pl. 6, fig. 3), P52689, both from North Sea Well 16/28–6RE, 4150.5 m. Early Aptian, P52688, from North Sea Well 20/2–2, 8300 ft, and P52690, from North Sea Well 15/30–3, 12830–12840 ft.

DISTRIBUTION. Mexico; subseabed Walvis Ridge and Angola Basin, southeastern Atlantic (DSDP Leg 40, sites 363 and 364 respectively); Central North Sea (Wells); Speeton, North Yorkshire, England; southeastern France; Spain; Southern U.S.S.R.

STRATIGRAPHY. Previously recorded as ranging from the Late Aptian to Early Albian (Caron, 1985; Banner and Desai, 1988), this species is reported here from the Early Aptian of the Central North Sea. The range given by Longoria (1974) must be extended.

Blefuscuiana infracretacea (Glaessner) *sensu lato*

REMARKS. As Longoria (1974, p. 59) wrote, this species-group name "has served as a 'waste-basket' name. . .; almost every Lower Cretaceous species with unknown affinity has been referred to this species". Re-examination of type specimens (which are illustrated here) at last enables it firmly to be placed in its correct genus and its species-characters to be recognised. This species is characterised by having 5–6 chambers in the last whorl, with a small, deep umbilicus; the flattened dorsal surface of this species has symmetrical, predominantly depressed chambers (about half as high as long when viewed dorsally) in the last whorl; the intercameral sutures are nearly radial.

B. infracretacea is distinguished from *B. daminiae s.l.* in having at least 5 chambers almost wholly visible on the ventral side with a correspondingly more pentagonal (rather than roughly quadrangular) test outline; it differs from *B. excelsa cumulus* by its lower spire (spiral side almost flat to moderately convex, compared to strongly convex; compare Pl. 4, figs. 4b, 5b, 6b, Pl. 5, figs. 1b, 2b, 3b & 5b, with Pl. 6, figs. 1b & 2b), and from *B. gorbachikae* (Longoria) by lacking the very strongly umbilically-directed last chambers diagnostic for that species (see Pl. 6, figs. 3a).

STRATIGRAPHY. Early to Late Aptian–?Albian, see subspecies below.

Blefuscuiana infracretacea (Glaessner) *sensu stricto*
Pl. 4, fig. 2a–c; Pl. 8, fig. 1a–c

1936 *Globigerina infracretacea* (Glaessner; 28, text-fig. 1.
1966 *Hedbergella infracretacea* (Glaessner), Glaessner: 179–184; Pl. 1, figs. 1a–3c.
1986 *Hedbergella aptica* (Agalarova), Gorbachik: 94; pl. 14, figs. 4, 5 (*not* 2, 3).
1988 *Blefuscuiana* cf. *aptica* (Agalarova), Banner & Desai: 160; pl. 3, figs. 4, 5a, 5b.

REMARKS. Glaessner (1966) reported that this species was originally collected in 1935 from dark calcareous clay, then dated as Albian, exposed in the valley of the River Ubin, at Ilskaya, Northwest Caucasus, U.S.S.R. He (1966, p. 180) carefully and thoroughly redescribed the gross morphology of the species, basing his work on 24 topotype specimens from the original collection. Three of these specimens were given to the U.S. National Museum, Washington, D.C., were claimed (1966, p. 184) to have been registered in the U.S.N.M. Catalogue No. 130 as specimens 642370–72, and were drawn for publication by L.B. Isham (Glaessner, 1966, pl. 1).

Isham's drawings showed the presence, on the test surface, of knobbly projections which could be either muricae or perforation-cones. The drawings showed perforations in a stylised way, and it was not clear whether the test was microperforate or macroperforate. Glaessner's redescription (1966) was equally vague on these points. Therefore, it was not possible to be sure if the species was a small, early *Hedbergella* or a late *Blefuscuiana*. Consequently, three topotype specimens, which had been collected by Glaessner in 1935, were borrowed from the U.S.N.M.; although they are catalogued as number 689757 (not as recorded by Glaessner, 1966), there can be no doubt, from their provenance and shape, that these are the specimens which were drawn by Isham, and they probably are metatypes.

Scanning Electron Photomicrography of these specimens (Pl. 4, fig. 2; Pl. 8, fig. 1) shows that Banner & Desai (1988, p. 160) and Hart *et al.* (1989, pp. 346–347) were wrong, that the species is not muricate or macroperforate, and is not to be referred to *Hedbergella*. Instead, it has irregularly spaced microperforations, which are covered by the most prominent perforation-cones yet seen in the Praehedbergellidae. Nothing like them exists in the post-Albian Globigerinacea, and only the Heterohelicacea had genera (*Cassigerinella, Guembelitria*) which possessed them in Late Cretaceous and younger times. The specimen called '*Hedbergella* cf. *aptica* (Agalarova)' by Gorbachik (1986, pl. 15, figs. 1, 2), from the 'Middle' Aptian of Alma, Crimea, U.S.S.R., has similar perforation-cones and may be the same as *B. infracretacea* from the Caucasus, but Gorbachik's illustrations do not show enough of the gross morphology to enable the reader to be certain.

Specimens identical to the Glaessner topotypes (Banner & Desai, 1988, pl. 3, figs. 4, 5a–b) confirm that the early whorls, on the dorsal surface of the test, are covered by thick lamellae of calcite which seal most of the early perforations, and that (ventrally) the primary aperture lacks a porticus. It is as though the species secreted the calcite not needed for its chambers on the chamber surfaces rather than around the aperture. The early dorsal perforation-cones are thus smothered in secondary lamellae, and those of the last chambers are weak because they have not yet been built up by the development of such lamellae—the cones are most prominent on the earlier chambers of the last whorl. These observations are confirmed by Glaessner's description (1966, p. 180): "The sculpture of the walls . . . first increases and then . . . decreases during growth of additional chambers. . . No projecting apertural lips have been observed." These support the emendation of the diagnosis of *Blefuscuiana*: these microperforate, non-muricate tests may have perforation-cones or a porticus or both.

Stratigraphy. *B. infracretacea* (Glaessner) has been found in the latest Aptian, *Acanthoplites nolani* zone, at Sarstedt, Saxony, Germany (Banner & Desai, 1988, p. 156, pl. 3, figs. 4, 5). The known range of the species, *sensu stricto*, is therefore Late Aptian ('Middle' Aptian in Gorbachik's (1986) sense is early Late Aptian); also, it may occur in the Albian if Glaessner's (1936) dating of the R. Ubin exposure was correct, but this has not yet been confirmed.

Blefuscuiana infracretacea (Glaessner) ***aptica*** (Agalarova)

Pl. 4, figs. 4a–c, 5a–c, 6a–c

1951 *Globigerina aptica* Agalarova: 49; pl. 8, figs. 9–11.
1960 *Globigerina infracretacea* Glaessner subsp. *trochoidea* Moullade: 136; pl. 2, figs. 21, 23–25.
1961 *Globigerina infracretacea* Glaessner subsp. *gargasiana* Moullade: 214 (new name).
1986 *Hedbergella aptica* (Agalarova); Gorbachik: 94; pl. 14, figs. 2, 3 (*not* 4–5).
1988 *Blefuscuiana aptica* (Agalarova); Banner & Desai: 160; pl. 5, figs. 4–7.

Remarks. This subspecies is morphologically almost identical to *B. infracretacea* (Glaessner) *sensu stricto* but possesses a porticus and lacks perforation-cones. The surfaces of the chamber walls are smooth. Agalarova (1951) noted that the proloculus stands out clearly on the dorsal side, showing that there is no heavy coating of secondary lamellae obscuring the early whorls; also, her original drawings show the presence of a porticus but give no indication of the presence of any other projections on the test surface.

Another morphological difference which is useful stratigraphically is that the typical *Blefuscuiana infracretacea aptica* is more tightly coiled, with a narrower umbilicus, than the phylogenetically more advanced *B. infracretacea sensu stricto*.

Provenance of types. P52701 (Pl. 4, figs. 4a–c), P52682 (Pl. 4, figs. 6a–c) and P52703, from North Sea Well 15/30–3, 12830–40 ft, Earliest Aptian; P52702 (Pl. 4, figs. 5a–c) and P52686 from North Sea Well 20/2–2, 8300 ft, Early Aptian; P52704, from North Sea Well 16/28–6RE, 4150.5 m, Early Aptian.

Distribution. Central North Sea (Wells), southern U.S.S.R. (Azerbaidzhan), S.E. France, Atlantic (sea-bed).

Stratigraphy. Early to Late Aptian. Agalarova's type specimens were obtained from the Aptian Khanaga Formation (eastern Azerbaidzhan), and Gorbachik (1986) figured specimens from the 'Middle' Aptian (early Late Aptian) of the Atlantic. Moullade (1960, 1961) obtained his specimens from the Late Aptian of south-east France. Banner & Desai (1988) illustrated it from the early Late Aptian of Speeton, Yorkshire, U.K. It has now been obtained from the Early Aptian of North Sea wells. *B. infracretacea aptica* appears to have older stratigraphic occurrences than *B. infracretacea s.s.*, and was probably its immediate ancestor.

Blefuscuiana laculata n.sp. *sensu lato*

Pl. 3, figs. 1a–c, 2a–c, 3a–c, 4, 5a–c

Name. After *laculatus, -a, -um*, four-cornered, referring to the test outline.

Diagnosis. Characterised by having 5 chambers in the last whorl, but with a test that is roughly quadrangular in outline, and by a broad, open umbilicus which the chambers do not overhang significantly.

Description. Test about 0.15–0.20 mm at its maximum diameter, comprising at least two whorls of chambers coiled in a low trochospire. There are 4–5 chambers in the penultimate whorl and 5 chambers in the final whorl. The spiral side is almost flat to slightly concave. The chambers are symmetrical and increase in size gradually with growth. The chambers are subglobular in the penultimate whorl, and subglobular to slightly depressed (about 2/3 as high as long when viewed from the spiral side) in the final whorl. The umbilicus is broad, but the aperture is a narrow slit. No perforation cones are known.

Remarks. *B. laculata* clearly possesses 5 chambers abutting the umbilicus in the last whorl (e.g. Pl. 3, figs. 1a–c), although only part of the first chamber of the last whorl may be seen ventrally. At first sight it resembles a species of *Praehedbergella*, and this, combined with its early stratigraphical range (i.e. Early Barremian) suggests that this species of *Blefuscuiana* had evolved directly from *Praehedbergella*.

The rate of enlargement of the chambers of the last whorl, as seen dorsally, is much slower than in *B. daminiae*; also the equatorial outline of *B. laculata* is more quadrangular than that of *B. daminiae*, which is more circular.

DISTRIBUTION. Central North Sea (wells); western Atlantic subseabed.

STRATIGRAPHY. Early Barremian.

Blefuscuiana laculata n.sp. *sensu stricto*

Pl. 3, figs. 1a–c, 2a–c

1979 *Clavihedbergella eocretacea* Neagu; Sigal: 290; pl. 3, figs. 31, ?30

DIAGNOSIS. Characterised by having a roughly quadrangular test outline, an open umbilicus, and intercameral sutures at the periphery of the test which form angles of about 120°–135°; the test surface lacks perforation cones.

PROVENANCE OF TYPES.
Holotype. P52724, Pl. 3, figs. 2a–c: from Central North Sea Well 20/2-2, 8680 ft, Early Barremian.
Paratype. P52725, Pl. 3, figs. 1a–c; from same sample as holotype.

REMARKS. *B. laculata s.s.* closely resembles *P. sigali s.s.* (see above) with which it occurs, the only significant difference being the number of chambers in the final whorl abutting the umbilicus (5 and 4 respectively; compare Pl. 3, figs. 1–2 with Pl. 2, fig. 2). The oldest known occurrence of both taxa is Early Barremian. Therefore, it seems likely that *P. sigali s.s.* gave rise to *B. laculata s.s.* shortly after the former taxon's first appearance; *P. sigali s.s.* itself ranges up to the Late Aptian.

DISTRIBUTION. Central North Sea (wells); subseabed Atlantic, offshore Portugal (DSDP Site 398).

STRATIGRAPHY. Sigal (1979) believed that this form was confined to the Barremian stage (as characterised by ammonites) in DSDP Site 398 (200 km off the coast of Portugal). We record it from the Early Barremian of the Central North Sea.

Blefuscuiana laculata alobata n.subsp.

Pl. 3, figs. 3a–c, 4, 5a–c

NAME. Referring to the less lobate test outline compared with the *B. laculata s.s.* (*loba* = lobe).

DIAGNOSIS. A subspecies of *B. laculata* characterised by having intercameral sutural angles at the periphery of about 130°–145°; the test surface lacks perforation cones.

PROVENANCE OF TYPES.
Holotype. P52726 (Pl. 3, figs. 3a–c), from central North Sea Well 20/2-2, 8680 m (Early Barremian).
Paratypes. P52727 (Pl. 3, figs. 5a–c), P52728 (Pl. 3, fig. 4), P52729, all from the same sample as the holotype.

REMARKS. This subspecies is distinguished from *B. laculata s.s.* in having less deeply depressed intercameral sutures at the periphery of the test. Although there is some overlap in the magnitude of this intercameral, peripheral angle between these taxa, the range that can be measured within a specimen is sufficient to distinguish clearly between the two subspecies.

The evolutionary relationship between *P. sigali s.s.* and *B. laculata s.s.* has been suggested above. Since the difference between *B. laculata s.s.* and *B. laculata alobata* (i.e., the magnitude of the intercameral sutural angle at the periphery of the test) is analogous to those between the subspecies of *P. sigali*, we regard it probable that the whole *P. sigali* species-group as having evolved, as a plexus, into that of *B. laculata*. However, we believe that it is worth distinguishing morphologically between the subspecies of each species because such distinctions clarify the taxonomy of the Praehedbergellidae as a whole and provide the potential for palaeo-environmental, or palaeobiogeographic, or biostratigraphic discrimination.

DISTRIBUTION. Central North Sea.

STRATIGRAPHY. Early Barremian.

Blefuscuiana occulta (Longoria) *sensu lato*

REMARKS. When Longoria erected *B. occulta*, he included only forms which lack perforation cones. Since we have found specimens in which perforation cones are present, but which are otherwise indistinguishable from *B. occulta sensu stricto*, we regard the species *sensu lato* to comprise both morphotypes.

STRATIGRAPHY. Late Barremian–Late Aptian (see subspecies below).

Blefuscuiana occulta (Longoria) *sensu stricto*

1974 *Hedbergella occulta* Longoria: 63–64; pl. 11, figs. 7–8; pl. 19, figs. 17–18; pl. 20, figs. 5–9, 17–18.
1976 *Hedbergella* aff. *planispira auct.* Sigal: pl. 2, figs. 1–2.
1988 *Blefuscuiana occulta* (Longoria); Banner and Desai: 162, pl. 6, figs. 8–12.

REMARKS. *B. occulta sensu stricto* is taken by us to be *B. occulta* as originally defined and illustrated (i.e. without perforation cones). A single specimen from the North Sea has 5½, rather than the usual 6–7 chambers in the last whorl.

DISTRIBUTION. Northern Mexico; Speeton, North Yorkshire, England; Central North Sea (Well 20/2-2, 8300 m, 8250 m); North Atlantic (DSDP Leg 47B, Site 398D, 200 m off the coast of Portugal, west of Oporto).

STRATIGRAPHY. Previously recorded from the Late Aptian of northern Mexico and Speeton, and from the Early Aptian of the North Atlantic, we have found this subspecies also to occur rarely in the Early Aptian drilled in the Central North Sea.

Blefuscuiana occulta (Longoria) ***perforocculta*** n.subsp.

Pl. 8, figs. 2a–c, 3

NAME. *Perfor-*, + *occulta*, the clearly perforate form of the species.

DIAGNOSIS. A subspecies of *B. occulta* characterised by having perforation cones marking the sites of the microperforations.

PROVENANCE OF TYPES.
Holotype. P52677 (Pl. 8, figs. 2a–c), from Central North Sea Well 20/2–2, 8300 m, Early Aptian.
Paratypes. P52678 (pl. 8, fig. 3), P52681, from the same sample as the holotype; P52679, from Central North Sea Well 15/30–3, 12830–12840 ft, Early Aptian, and P52680, from Central North Sea Well 16/28–6RE, 4014.37 m, Late Aptian.

DESCRIPTION. Test about 0.20–0.25 mm at its maximum diameter, comprising about 3 whorls coiled in a low trochospire. There are 5½–7 chambers in each of the penultimate and last whorls. The spiral side is almost flat. The intercameral sutures are depressed to form angles of about 130°–140° at the periphery of the test. The chambers are symmetrical, increase in size gradually with growth, and are typically subglobular. The umbilicus is broad and the aperture appears to be a narrow slit. Perforation cones are present dorsally and ventrally on the chambers of the last whorl.

REMARKS. This form is rare in the Late Barremian (so far found in beds of this age only in Well 20/2–2 at 8370 ft), but it occurs quite commonly in beds considered to be Early Aptian and it ranges up into Late Aptian sediments. Therefore, it appears older than *B. occulta sensu stricto*, and to acme earlier and to disappear earlier; it may prove to be the phylogenetically older form of the species.

DISTRIBUTION. Central North Sea (wells).

STRATIGRAPHY. Late Barremian–Late Aptian.

Blefuscuiana praesimilis n.sp. Pl. 8, figs. 4a–c, 5, 6

NAME. After similarity to *Lilliputianella similis*, which it precedes stratigraphically.

DIAGNOSIS. Characterised by a very broad umbilicus, subglobular chambers which become nearly as high as long when viewed dorsally, an almost planar dorsal side with depressed sutures, and a markedly lobulate equatorial periphery.

PROVENANCE OF TYPES.
Holotype. P52691 (Pl. 8, figs. 4a–b) from Central North Sea Well 20/2–2, 8680 ft, Early Barremian.
Paratypes. P52692 (Pl. 8, fig. 5), P52694, both from same sample as holotype; P52693 (Pl. 8, fig. 6), P52695, from the same well, at 8600 ft, also Early Barremian.

DESCRIPTION. Test about 0.15–0.20 mm at its maximum diameter, comprising about 2 whorls coiled in a low trochospire. There are about 5–6 chambers in the last whorl, but this is an ontogenetic increase as the penultimate may have only 4–5. The spiral side is almost flat, slightly concave or slightly convex, with depressed sutures, and the intercameral sutures form angles of about 140° at the periphery of the test, which becomes markedly lobulate. The chambers are symmetrical and increase in size gradually with growth. They are typically globular to slightly depressed (about 2/3 as high as long when viewed from the spiral side) in the last whorl. The umbilicus is very broad (about one-third of the test diameter). The aperture appears to be a narrow slit. Perforation cones have not been found on this species.

REMARKS. This species resembles *Lilliputianella similis* (compare Pl. 8, figs. 4–6 with Pl. 8, fig. 8), and is probably immediately ancestral to it, even though it is not yet known from the late Barremian. *B. praesimilis* is distinguished from *B. aptiana s.l.* in having a broader umbilicus.

DISTRIBUTION. Central North Sea (wells).

STRATIGRAPHY. Early Barremian.

Blefuscuiana rudis n.sp. Pl. 5, figs. 1a–c, 2a–c, 5a–c

NAME. After *rudis*, rough, unpolished, referring to the test surface which possesses perforation cones.

DIAGNOSIS. A bulky test with marked dorsal convexity and weakly depressed sutures, early chambers which are subglobular, but with predominantly depressed chambers in the last whorl (about half as high as long when viewed dorsally), and with perforation cones.

PROVENANCE OF TYPES.
Holotype. P52713 (Pl. 5, figs. 1a–c), from Central North Sea Well 16/28–6RE, 4275 m (Early Barremian).
Paratypes. P52714 (Pl. 5, figs. 5a–c), from same sample as holotype; P52715 (Pl. 5, figs. 2a–c), Central North Sea Well 20/2–2, 8250 ft (Early Aptian); P52716, Central North Sea Well 15/30–3, 12830–12840 ft (Early Aptian).

DESCRIPTION. Test about 0.15–0.30 mm at its maximum diameter, comprising about 3 whorls. There are 5–6 (commonly 6) chambers in each of the penultimate and last whorls. The spiral side is strongly convex. The intercameral sutures are weakly depressed and form intercameral angles of 150° or more at the periphery of the test. The chambers are symmetrical and increase in size gradually with growth; they are predominantly depressed in the final whorl, commonly being about half as high as long (when viewed on the dorsal side), but the penultimate chamber may be only slightly depressed (about 2/3 as high as long when viewed dorsally), while the last chamber may be subglobular. The umbilicus is small and deep and the aperture appears to be a narrow slit. Perforation cones are present on all chambers of the last whorl.

REMARKS. This species is distinctive because of its compact, almost plano-convex test, with low, depressed, symmetrical chambers, weakly depressed intercameral sutures, and a spire which appears to open only slowly when seen in dorsal view. The typical form has well developed perforation cones, but another subspecies, with a smooth surface, has not yet been found.

DISTRIBUTION. Central North Sea (wells).

STRATIGRAPHY. Early Barremian–Early Aptian.

Blefuscuiana whittakeri n.sp. Pl. 5, figs. 3a–c, 4

NAME. For J.E. Whittaker, The Natural History Museum, London, for his help in preparing the environmental chamber SEM photomicrographs of *B. infracretacea* (Glaessner) and for his enthusiastic support in this project.

DIAGNOSIS. Characterised by high, rapidly enlarging chambers, about 5 in each of the later whorls, forming a robust test with virtually radial and straight intercameral sutures, a flattened dorsal side and a very small ventral umbilicus.

PROVENANCE OF TYPES.
Holotype. P52717 (Pl. 5, figs. 3a–c, 4), from North Sea Well 15/30–3, 12830–12840 ft, Early Aptian.
Paratypes. P52718, from same sample as holotype; P52719 and P52720, from North Sea Well 20/2–2, 8250 ft and 8300 ft

respectively, both Early Aptian; P52721, P52722 and P52723, all from North Sea Well 16/28–6RE, 4250 m, 4225 m and 4275 m respectively, all Early Barremian.

DESCRIPTION. Test about 0.10 mm to 0.25 mm in maximum diameter; about three whorls of inflated, subglobular chambers, forming a test which is slightly convex or flattened dorsally, and convex ventrally with a small but deep umbilicus. The chambers enlarge rapidly, so that the last whorl increases the diameter of the test by more than 50% (i.e. from about 60% of the final diameter to 100%); the chambers are symmetrical (highest in their mid-parts) and are high when seen dorsally, becoming as high as long. The dorsal and ventral intercameral sutures are virtually straight and radial, and the terminal face is high, radial and flattened. The intercameral sutures are moderately depressed and make depressions of about 150° at the equatorial periphery. The aperture is a low slit. The surface of the typical form of the species is covered by low perforation cones (Pl. 5, fig. 4).

REMARKS. This species most clearly differs from *B. rudis* by its undepressed chambers which more rapidly enlarge and consequently increase the diameter of the test more rapidly (compare Pl. 5, fig. 3b with Pl. 5, figs. 1c, 2c and 5c), and by its narrower umbilicus; also, its dorsal intercameral sutures are straighter, more radial, and the dorsal surface of the test is flatter than in *B. rudis*. A form of this species which lacks perforation cones has not yet been recognised.

DISTRIBUTION. Central North Sea (Wells).

STRATIGRAPHY. Early Barremian–Late Aptian.

Genus **LILLIPUTIANELLA** Banner and Desai, 1988

TYPE SPECIES: *Lilliputianella longorii* Banner and Desai, 1988.

Lilliputianella eocretacea (Neagu) Pl. 6, fig. 8, pl. 8, figs. 7a–c

1975 *Clavihedbergella eocretacea* Neagu: 112–113; pl. 89, figs. 1–10, text-fig. 20.

PROVENANCE OF TYPES. P52731 (Pl. 8, figs. 7a–c), North Sea Well 15/30–3, 12830–12840 ft, Early Aptian; P52732 (Pl. 6, fig. 8), North Sea Well 16/28–6RE, 4160.7 m, Early Aptian.

REMARKS. This species has less strongly depressed intercameral sutures, a smaller umbilicus, and the early chambers in the last whorl are depressed, not high or radially elongate.

This species was originally found (Neagu, 1975) in Romanian strata believed to be Late Barremian in age; this would be the stratigraphically oldest occurrence of *Lilliputianella*, but it needs confirmation. In the North Sea area and elsewhere (e.g. Longoria, 1974; Banner and Desai, 1988) this genus is not yet known from below the Aptian.

Neagu (1975) believed this species to have been evolved directly from *Praehedbergella sigali*; his species was recorded rarely to have four chambers in the last whorl, which would support this idea, but normally to have five (as in the holotype figured by Neagu, 1975, and in one hypotype, P52731) and rarely six (as in our P52732). It probably evolved in Late Barremian time from phylogenetically early *Blefuscuiana* (Banner & Desai, 1988).

DISTRIBUTION. Romania; Central North Sea (wells).

STRATIGRAPHY. Late Barremian?–Early Aptian.

Lilliputianella similis (Longoria) Pl. 8, figs. 8a–c

1974 *Hedbergella similis* Longoria: 68–69; pl. 16, figs. 10–21; pl. 18, figs. 12–13; pl. 23, figs. 14–16.

1981 *Hedbergella similis* Longoria; Tronchetti: 141–242; pl. 37, fig. 1–7.

1988 *Lilliputianella similis* (Longoria); Banner and Desai: 169; pl. 8, figs. 8–9.

PROVENANCE OF TYPES. P52730 (Pl. 8, figs. 8a–c), from North Sea Well 20/2–2, 8300 ft (Earliest Aptian).

REMARKS. The North Sea subseabed specimens do not differ in any significant respect from those recorded by Longoria (1974) or from those previously recovered from outcrop at Speeton (Banner & Desai, 1988).

DISTRIBUTION. Northern Mexico; France; Speeton, North Yorkshire, England; Central North Sea (Well 20/2–2, 8300 ft).

STRATIGRAPHY. Previously recorded from the Early to basal Late Aptian of Mexico, from the Late Aptian of France and the basal Late Aptian of Speeton (Yorkshire), it also occurs in the subseabed Earliest Aptian of the North Sea area.

THE BIOSTRATIGRAPHIC SIGNIFICANCE OF NORTH SEA BARREMIAN-APTIAN PRAEHEDBERGELLIDAE

This reconnaissance has recognised the occurrence of species of *Praehedbergella* and *Blefuscuiana* in sediments from Early Barremian to Late Aptian age, and, from Early Aptian strata, *Lilliputianella*. The planispiral, schackoinid genera *Blowiella* Kretchmar and Gorbachik and *Leupoldina* Bolli, although known from the Late Aptian outcrop of Speeton and from Barremian and Early Aptian beds of more southerly occurrence (Banner and Desai, 1988), have not yet been found by us in well samples from the Central North Sea. The recognised distributions of the species which have been found, in the samples from the wells studied, are shown on Figs. 1–3, and the biostratigraphic results are synthesised and summarised on Fig. 4.

One of us (PC) has worked on North Sea Lower Cretaceous planktonic foraminifera for a number of years. This has allowed the development and utilisation of a succession of five planktonic foraminiferal assemblages, within the Barremian–Aptian interval, for subsurface stratigraphical subdivision and correlation. This has resulted in the recognition of the stratigraphic divisions of the subsurface North Sea Early Cretaceous sequences and the dating of these divisions from combined foraminiferal, nannofossil and dinocyst evidence. Several of these assemblages have already been reported by previous workers on the micropalaeontology of the North Sea area (see the *Previous Work* discussed above), though the species were loosely referred to as '*Hedbergella infracretacea*', '*Hedbergella D9* of Hecht' and so on. As their taxonomy has now been revised, the assemblages can be more precisely described, and the stratigraphically significant assemblages

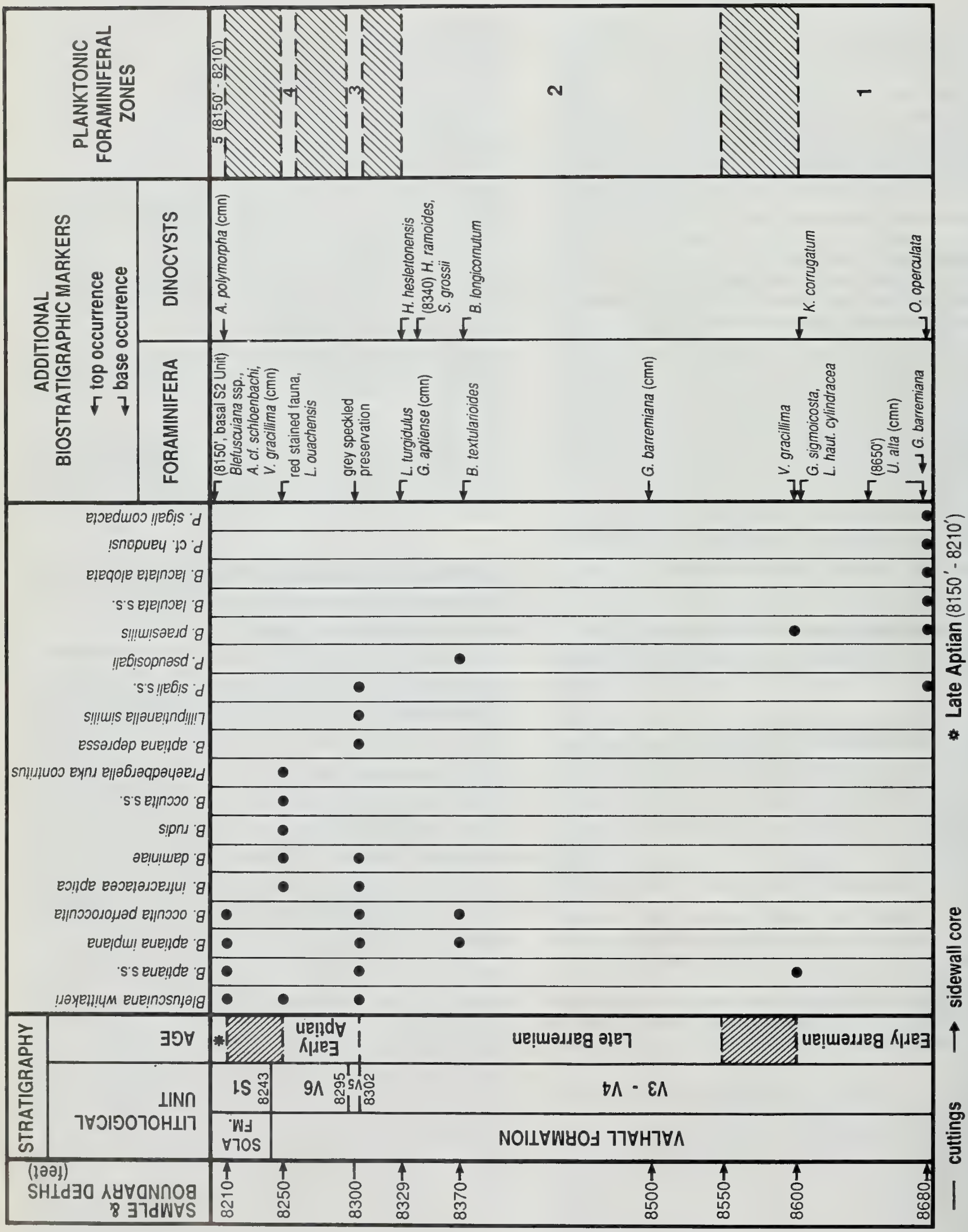

Fig. 1 Occurrences of taxa of the Praehedbergellidae in Central North Sea Well 20/2-2, Lower Barremian to Upper Aptian. Depths in stratigraphy columns refer to wireline log depths. Cross hatching refers to unstudied intervals between samples, with dashed horizontal lines indicating limits of proven age units. Boundaries marked by continuous lines have been taken at log features.

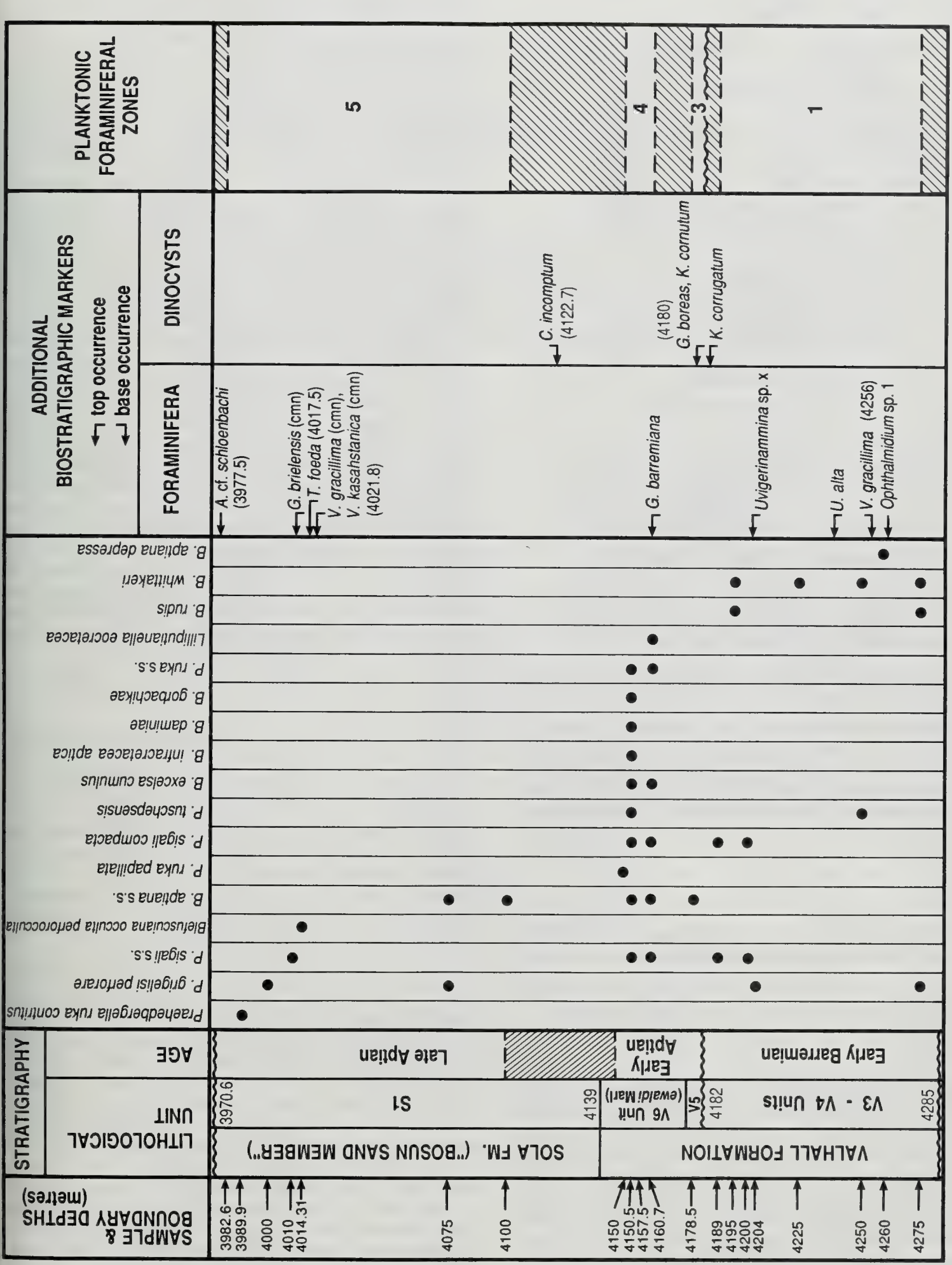

Fig. 2 Occurrences of taxa of the Praehedbergellidae in Central North Well 16/28-6RE, Lower Barremian to Upper Aptian. Depths in stratigraphy columns refer to wireline log depths.

12,830 - 40 feet	SAMPLE (core)	
Valhall Formation V6 Unit (*ewaldi* Marl)	LITHOLOGICAL UNIT	STRATIGRAPHY
Early Aptian	AGE	
●	*B. aptiana* s.s.	
●	*B rudis*	
●	*B. whittakeri*	
●	*B. occulta perforocculta*	
●	*Lilliputianella eocretacea*	
●	*B. excelsa cumulus*	
●	*B. infracretacea aptica*	
●	*B. daminiae*	
●	*B. gorbachikae*	
4	PLANKTONIC FORAMINIFERAL ZONE	

Fig. 3 Occurrences of red-stained taxa of the Praehedbergellidae in the Lower Aptian, *ewaldi* marl, lithological unit V6, Valhall formation, in Well 15/30–3, Central North Sea.

can be used to define a succession of five informal biozones as outlined below.

In the biozonal descriptions below, 'appearances' refer to stratigraphic bases (last downhole *in situ*, uncaved occurrences) while 'disappearances' refer to stratigraphic tops (first downhole occurrences). The associated occurrences of stratigraphically useful benthonic foraminifera, dinocysts and nannofossils are identified by the use of 'F', 'D' and 'N' respectively.

Zone 1

TAXA RESTRICTED TO ZONE 1. *Blefuscuiana praesimilis, B. laculata s.s., B. laculata alobata, Praehedbergella* cf *handousi*.

TAXA APPEARING IN ZONE 1. As above, plus *Praehedbergella grigelisi perforare, P. sigali s.s., P. sigali compacta, P. tuschepsensis, Blefuscuiana aptiana depressa, B. rudis, B. whittakeri*.

REMARKS. This zone contains the oldest common occurrence of Lower Cretaceous planktonic foraminifera in the North Sea basin, although rare, isolated specimens may occur below Zone 1, in the Hauterivian. This acme consists of members of the Praehedbergellidae, as the Favusellacea are as yet unknown from strata of Barremian age in the North Sea. The praehedbergellid influx is seen over a wide area, in well sections from west of Shetland to the central North Sea, and it forms a very useful biostratigraphic unit for correlation.

AGE AND STRATIGRAPHY. An Early Barremian age is indicated by the co-occurring benthonic foraminifera and dinocysts and by the correlated nannofossils. The top of Zone 1 coincides with the disappearances of *Kleithriasphaeridium corrugatum* (D) and *Gavelinella sigmoicosta* (F), and its base coincides with the appearances of *Gavelinella barremiana* (F), *Valvulineria gracillima* (F) and *Odontochitina operculata* (D). These overlapping occurrences indicate an Early Barremian age. Typically also occurring within Zone 1 is an abundance of *Uvigerinammina* spp referable to '*U.* sp. X' King *et al.* (1989) and *U. alta* (identified variously as *U. moesiana* or '*U. moesiana* subsp. A' in industry reports).

Zone 1 occurs within the Valhall Formation V3 Unit typically shortly beneath the Munk Marl Bed high-gamma claystone. In condensed sequences, on structural highs, the praehedbergellid association (together with the benthonic foraminifera mentioned above) occurs within a limestone facies referred to the Tuxen Formation (Jensen *et al.*, 1986; Crittenden *et al.*, 1991). In this facies, other benthonic foraminifera such as *Trocholina infragranulata, Aulotortus neocomianus, Patellina subcretacea* and *Spirillina* spp are common. Co-occurring nannofossil assemblages are stratigraphically useful. The zone contains the tops of *Conusphaera oblongata* and *C. salebrosus* (N), in downhole succession (Jakubowski, 1987). The latter event was dated as Early Barremian by Jakubowski (1987) and by Taylor (1982). The first downhole occurrences of *Stradnerlithus comptus* (N), common *Diazmolithus lehmanni* (N) and *Lithastrinus septentrionalis* (N) occur beneath the base of Zone 1, marking sediments of earliest Barremian age immediately below the base of that zone. *S. comptus* has been recorded from the *variabilis* ammonite zone (basal Barremian) at Speeton (Jakubowski, 1987). The latter nannofossil association occurs with the top of *Meandrospira washitensis* (F), an event used to mark the basal Barremian in the North Sea.

Zone 2

TAXA RESTRICTED TO ZONE 2. *Praehedbergella pseudosigali*.

TAXA APPEARING IN ZONE 2. As above, plus *Blefuscuiana aptiana aptiana, B. aptiana implana, B. occulta perforocculta*.

REMARKS. This zone represents the interval between the abundant and diverse assemblages of Zones 1 and 3, and typically contains relatively low numbers of taxa such as *Blefuscuiana aptiana s.s., B. aptiana implana* and *Praehedbergella grigelisi perforare*. The zone is difficult to identify unless it is in sequence with the other zones.

AGE AND STRATIGRAPHY. Zone 2 ranges from shortly beneath the Munk Marl Bed up to the top of the Barremian. The Munk Marl Bed is believed to correlate with the Batterton facies of eastern England (Speeton) and Germany, which is dated as late Early to early Middle Barremian (mid-*elegans* to mid-*fissicostatus* ammonite zones) (Rawson and Mutterlose, 1983). There is doubt whether the top of Zone 2 is Middle Barremian in age or whether it extends into the Late Barremian; this is partly due to the different subdivisions of the Barremian that are used (see, e.g. King *et al.*, 1989) and partly due to the possibility that the Late Barremian beds may be partly or wholly absent over much of the North Sea Basin. However, the top of Zone 2 corresponds to the first downhole occurrence of *Nannoconus abundans* (N), usually taken to mark the top of the Upper Barremian, and this is shortly succeeded downhole by the tops of *N. borealis* and

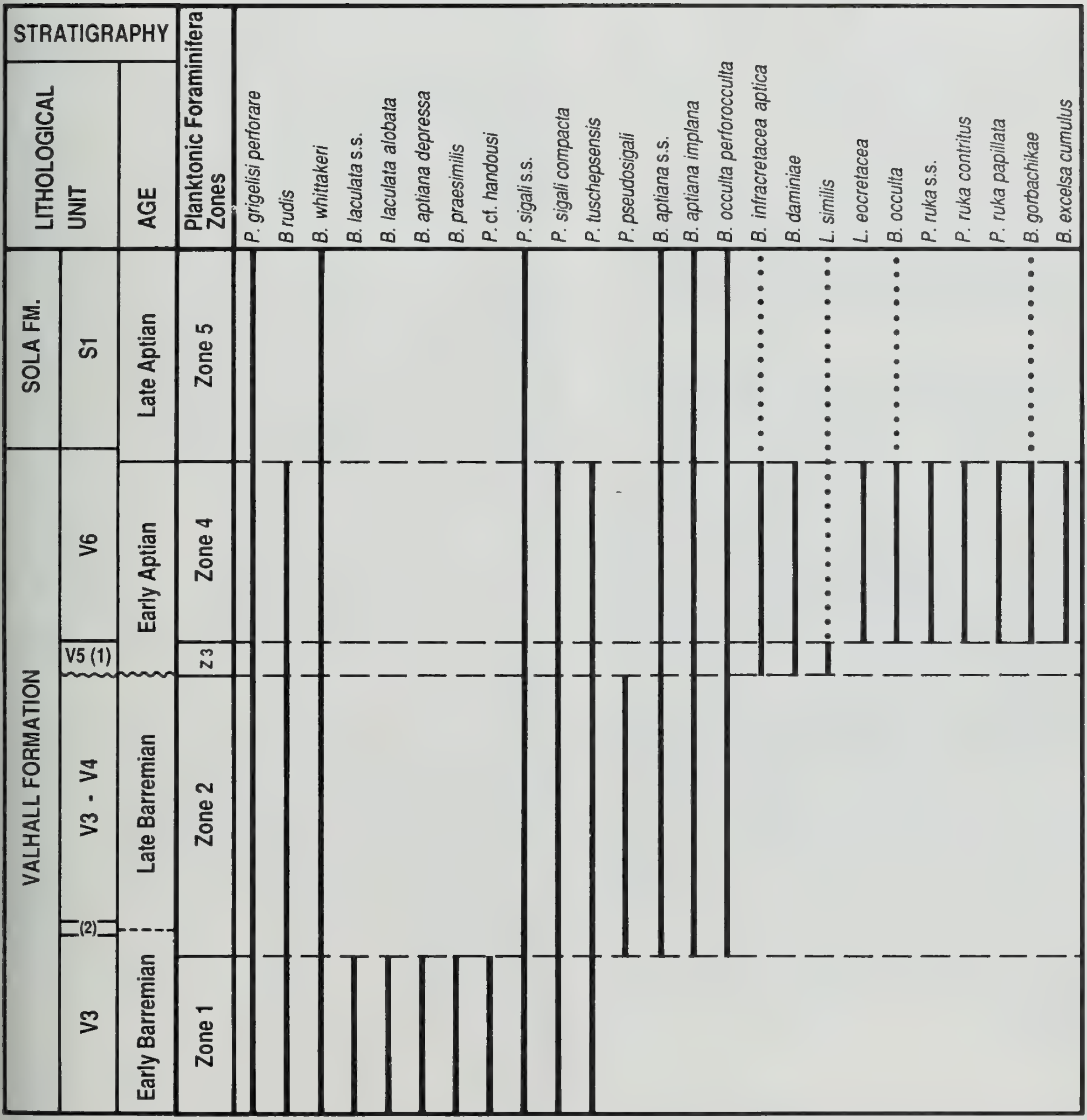

Fig. 4 Summary stratigraphical distribution of Central North Sea Barremian–Aptian Praehedbergellidae. Continuous stratigraphical lines: ranges as observed in samples from wells 15/30-3, 16/28-6RE and 20/2-2. Dotted stratigraphical lines: ranges extended from outcrop occurrences known elsewhere in the North Sea general region. (1) = Fischschiefer Member; (2) = Munk Marl Bed.

Conusphaera rothii (N), taken to indicate Middle Barremian age (Jakubowski, 1987).

Other taxa typically first occurring in Zone 2 include *Brizalina textularioides* (F) and *Gavelinella barremiana* (F). The first downhole occurrences of *Heslertonia heslertonensis, Hystrichodinium ramoides* and *Batioladinium longicornutum* (all D) occur at the top of the zone.

Zone 3

TAXA RESTRICTED TO ZONE 3. None.

TAXA APPEARING IN ZONE 3. *Lilliputianella similis* (not yet known above this zone in the North Sea wells, but known from younger beds at Speeton and elsewhere), *Blefuscuiana infracretacea aptica, B. daminiae.*

REMARKS. The planktonic foraminiferal assemblages of this zone are typically coloured grey with dark speckles of organic material, reflecting their origin in the organic-rich claystones of the V5 Unit. The praehedbergellids of this zone are often dominated numerically by *Blefuscuiana aptiana*, but seem also to be characterised by the appearance of the genus *Lilliputianella.*

AGE AND STRATIGRAPHY. This zone is restricted to the Fischschiefer Member (V5 Unit) of the Valhall Formation, a claystone unit distinguished by its high organic content with concomitant high gamma wireline log values and by large quantities of amorphous organic matter in the palynological assemblages. The Fischschiefer of the Lower Saxony Basin is generally considered to be of earliest Aptian age (cited by King *et al.*, 1989, p. 399, as belonging to the early *deshayesi* and *forbesi* ammonite zones), and its correlation with Unit V5, characterised by a horizon of abundance of '*Hedbergella* D9', has been noted by Crittenden *et al.* (1991). King *et al.* (1989) included it within 'Zone FCS7', the '*Hedbergella infracretacea* Zone'.

Associated benthonic foraminifera are not common, probably because of dysoxic conditions at or in the seabed during the time of deposition. The most consistently associated species is *Lenticulina kugleri* (F), with rare *Gavelinella barremiana* (F), even though the lowest and highest occurrences of the latter species were used by King *et al.* (1989, p. 399) to mark their subzone FCS6a, thought by them to be 'Middle Barremian'. The latter probably equates to the numerical increase of *G. barremiana* seen in the Barremian, but the species does range, in low numbers, into the Early Aptian, V6 Unit. Zone 3 is situated between the stratigraphic top common occurrence of *Lithiraphidites morayfirthensis* (N) (which occurs in Zone 4) and the stratigraphic base occurrence of this species.

Zone 4

TAXA RESTRICTED TO ZONE 4. *Praehedbergella ruka ruka, P. ruka contritus, P. ruka papillata, Blefuscuiana excelsa cumulus, Lilliputianella eocretacea.*

TAXA APPEARING IN ZONE 4. As above, plus *Blefuscuiana gorbachikae, B. occulta.*

TAXA DISAPPEARING IN ZONE 4. *Blefuscuiana daminiae, B. rudis, Praehedbergella sigali compacta, P. tuschepsensis.*

REMARKS. This zone is easily recognised in the North Sea by its abundance and diversity of praehedbergellid foraminifera and by the red colouration of its sediment and microfossils. Planktonic foraminifera can be so abundant as to form a fossil 'Globigerina ooze'; this also occurs in Heligoland, where the same deposit is called the 'Globigerinen-Kalk'. Consequently, the occurrence of the praehedbergellid assemblage of this zone has been previously reported by biostratigraphers, but the species present have been grouped as '*Hedbergella infracretacea*' (King *et al.*, 1989) or '*Hedbergella* D11 Hecht' (Crittenden *et al.*, 1991).

AGE AND STRATIGRAPHY. This zone is restricted to the red-brown, marl-limestone V6 Unit of the Valhall Formation, which has been correlated with the '*ewaldi* Marl' of Germany, Heligoland and eastern England (e.g. King *et al.*, 1989, who also included it in their 'subzone FCS7b', the FCS7b1 unit). The red-stained planktonic foraminiferal association of Zone 4 often contains abundances of *Valvulineria gracillima* (F). The Zone can also be noted by the disappearances of *Gavelinella barremiana* and *Lenticulina ouachensis* (F). Zone 4 also contains the first downhole common occurrence of *Lithiraphidites morayfirthensis* (N), an event used as an Early Aptian marker in the North Sea (Jakubowski, 1987). For this reason, Zone 4 is marked as being Early Aptian on Figure 4. However, a probably equivalent 'Red Mudstone' in Block 81 has ostracod assemblages which have been dated as Late Aptian (*nutfieldensis* and *martinioides* ammonite zones) as cited by Lott *et al.* (1985). In consequence, it is possible that Zone 4 may yet prove to span the Early Aptian–Late Aptian boundary.

Zone 5

TAXA RESTRICTED TO ZONE 5 OR APPEARING IN THIS ZONE. None known as yet, but see below.

TAXA DISAPPEARING IN THIS ZONE. *Blefuscuiana aptiana implana, B. occulta perforocculta, B. whittakeri, Praehedbergella sigali sigali.*

REMARKS. Zone 5 contains a less diverse assemblage than Zone 4, as some taxa appear to become extinct at its base, and the assemblages contain much less abundant specimens. Apparently due to palaeoceanographic circumstances which are, as yet, not elucidated, this zone contains the last occurrences of Praehedbergellidae in the North Sea wells. Further work must continue, especially on the correlation of this zone with the assemblages from Speeton (Banner and Desai, 1988) and its possible correlation with the *Leupoldina cabri* Zone or younger Aptian zones of more southerly outcrops. The praehedbergellids of Zone 5 are typically green, grey or brown stained, as they originate from the green-grey claystones of the lower Sola Formation (S1 Unit).

AGE AND STRATIGRAPHY. Zone 5 may be equated to the uppermost part of the '*Hedbergella infracretacea* Zone' (uppermost FCN7 or FCS7 Zones, the FCS7b2 or 'green *Hedbergella*' unit) of King *et al.* (1989, p. 398), which these authors suggested to be of middle Late Aptian (*nutfieldensis* ammonite zone) age (King *et al.*, 1989, figs. 8.3, 8.7). The age-equivalent assemblage had been reported by Lott *et al.* (1985, as '*Hedbergella infracretacea*') from well 81/40, in the Southern North Sea, and also dated as Late Aptian. Crittenden's (1987) green-stained '*Hedbergella infracretacea*' assemblage, also from Southern North Sea wells, is also referable to Zone 5; Crittenden (1987) also suggested a Late Aptian age (*nolani-jacobi* ammonite zones) for this interval from its correlation with Germany. Crittenden *et al.* (1991) interpreted the age of the Northern North Sea green-stained '*H. infracretacea*' assemblage as being referable to the *nutfieldensis* ammonite zone, and considered the influx of planktonic foraminifera in the North Sea area to have been a transgressive event. A Late Aptian age is corroborated for the zone by the first downhole occurrences of *Aptea polymorpha* (D) and *Dingodinium albertii* (D) (Crittenden *et al.*, 1991). The downhole increase in *Ellipsoidictyum imperfectum* (cigar-shaped D), cited by these authors to occur with these events, actually occurs above, in the Albian.

The Central North Sea praehedbergellid assemblages reported in the present paper are clearly of the same age as the assemblages noted above in previous records. However, as the top of Zone 5 usually occurs below the highest (first downhole) palynological evidence of Upper Aptian, an intra-Late Aptian age for the upper boundary of this zone is preferred.

Associated with the praehedbergellids of Zone 5 are the first downhole occurrences of the benthic foraminifera (F) *Astacolus* cf *schloenbachi, Saracenaria spinosa, Gavelinella brielensis*, common *Valvulineria gracillima* and common *V. kasahstanica*. The benthic foraminifera, like the planktonic species, are commonly green stained.

Nannofossil occurrences provide important evidence for the age of this zone. Zone 5 contains the first downhole occurrences (stratigraphic tops) of *Micrantholithus hoschulzii, M. obtusus* and *Eprolithus varolii* (all N) with an increase in nannoconids (Jakubowski, 1987). Sissingh (1977) and Perch-Neilsen (1979) used the stratigraphic top of *M. hoschulzii* to define the top of the Lower Aptian, but later Perch-Nielsen (1985, p. 359) drew its range (and that of *M. obtusus*) to reach to the top of the Aptian; Jakubowski (1987) and Taylor (1982) have both recorded the first downhole occurrence of *M. hoschulzii* within the Upper Aptian of the North Sea area. Zone 5 contains the base occurrence of *Parhabdolithus angustus* (N); this is a well documented datum occurring near the base of the Upper Aptian worldwide (e.g. Perch-Nielsen, 1985, p. 341). This is shortly preceeded downsection by the top common *Rhagodiscus asper* (N), an event known within the Upper Aptian of onshore Germany (*nutfieldensis* ammonite zone) (Jakubowski, 1987). This supports the placement of Zone 5 within the *nutfieldensis* ammonite zone, Late Aptian.

Conclusions

The five informal zones which this reconnaissance has recognised span the interval from Early Barremian to Late Aptian. Beds of earliest Aptian age seem to be most easily recognised by the lowest stratigraphical occurrences of (morphologically primitive) *Lilliputianella*. The appearance of certain nannoplankton (e.g. *Rhagodiscus asper*) in the Late Aptian beds has been thought (Jakubowski, 1987) to reflect an influx of warm Tethyan water at this time; the same northward influx (deflected to its left by the Coriolis effect) may have brought *Leupoldina* and *Blowiella* to the west, near Speeton, but may have had little influence more eastwards, in the Central North Sea area. This may explain why these genera have not been found yet in Late Aptian beds of Central and Northern North Sea wells. It must also be remembered that Speeton is in a separate basin (the Southern North Sea Basin) from the basins of the Northern North Sea and Central North Sea, and is separated from them by the Mid North Sea High; the latter may have acted as a barrier to current flow and to microplanktonic migration. Also, differences in palaeoclimate may have had their effect. However, the species-group taxa of the Praehedbergellidae have considerable potential biostratigraphical value in the Barremian–Aptian interval of North Sea sediments, and their study should be pursued beyond this reconnaissance.

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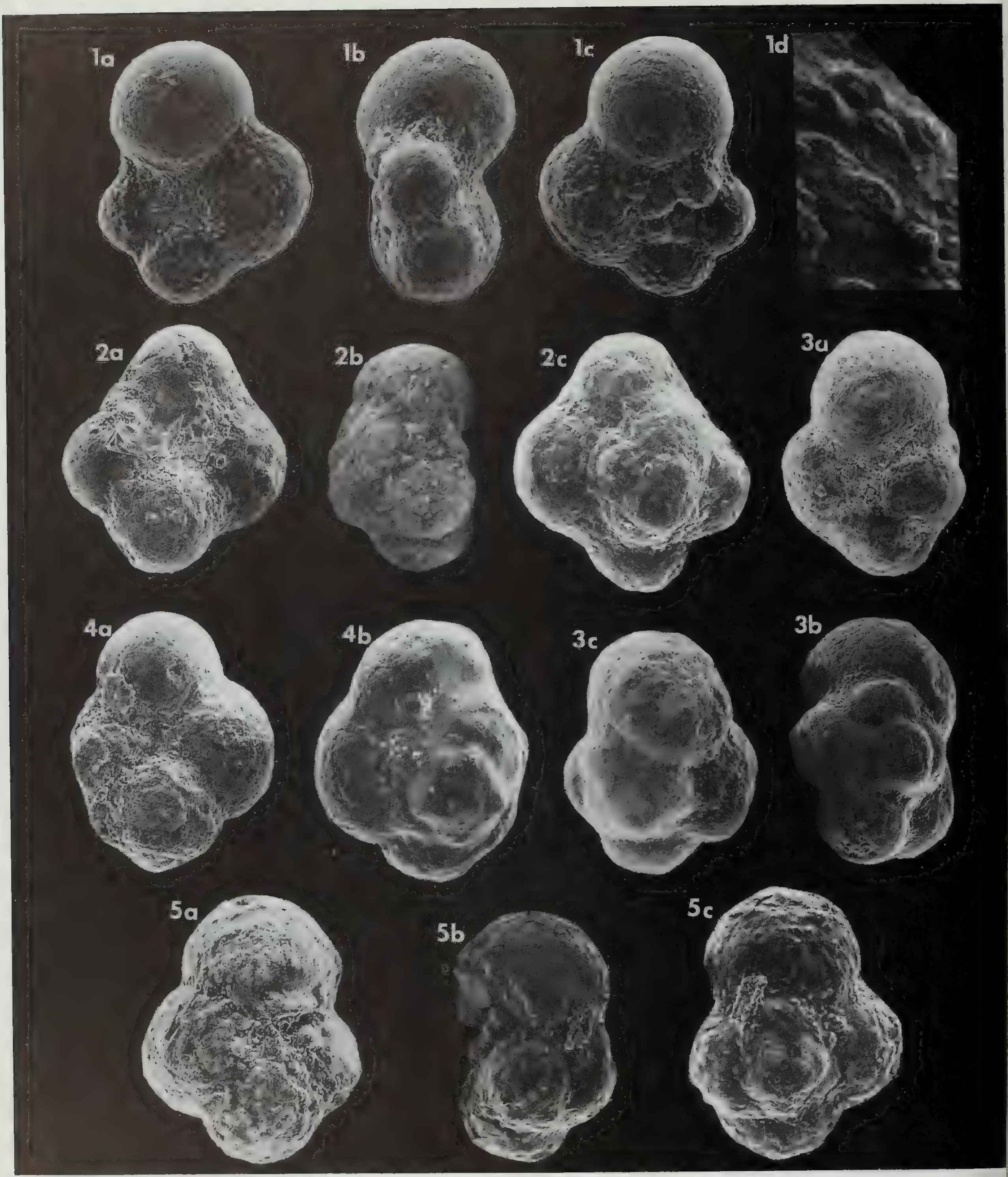


Plate 1

Fig.1 *Praehedbergella grigelisi* (Banner & Desai) *perforare* n.ssp. Early Aptian, Well 20/2–2, 8300 ft: a–c, ventral, peripheral and dorsal views of holotype, P52758, X 220; 1 d, perforation cones on holotype, X 2500.

Fig. 2 *Praehedbergella ruka* n.sp. *sensu stricto*. Early Aptian, Well 16/28–6RE, 4157.5 m: 2a–c, ventral, peripheral and dorsal views of holotype, P52739, X 315.

Figs 3–4 *Praehedbergella ruka contritus* n.ssp. 3a–c, Well 16/28–6RE, 3989.5 m, Late Aptian. Ventral, peripheral and dorsal views of holotype, P52737, X 330, 4a–b, Well 20/2–2, 8250 ft, Early Aptian. Ventral and dorsal views of paratype, P52738, X 300.

Fig. 5 *Praehedbergella ruka papillata* n.ssp. Early Aptian, Well 16/28–6RE, 4150 m: a–c, ventral, peripheral and dorsal views of holotype, P52736, X 315.

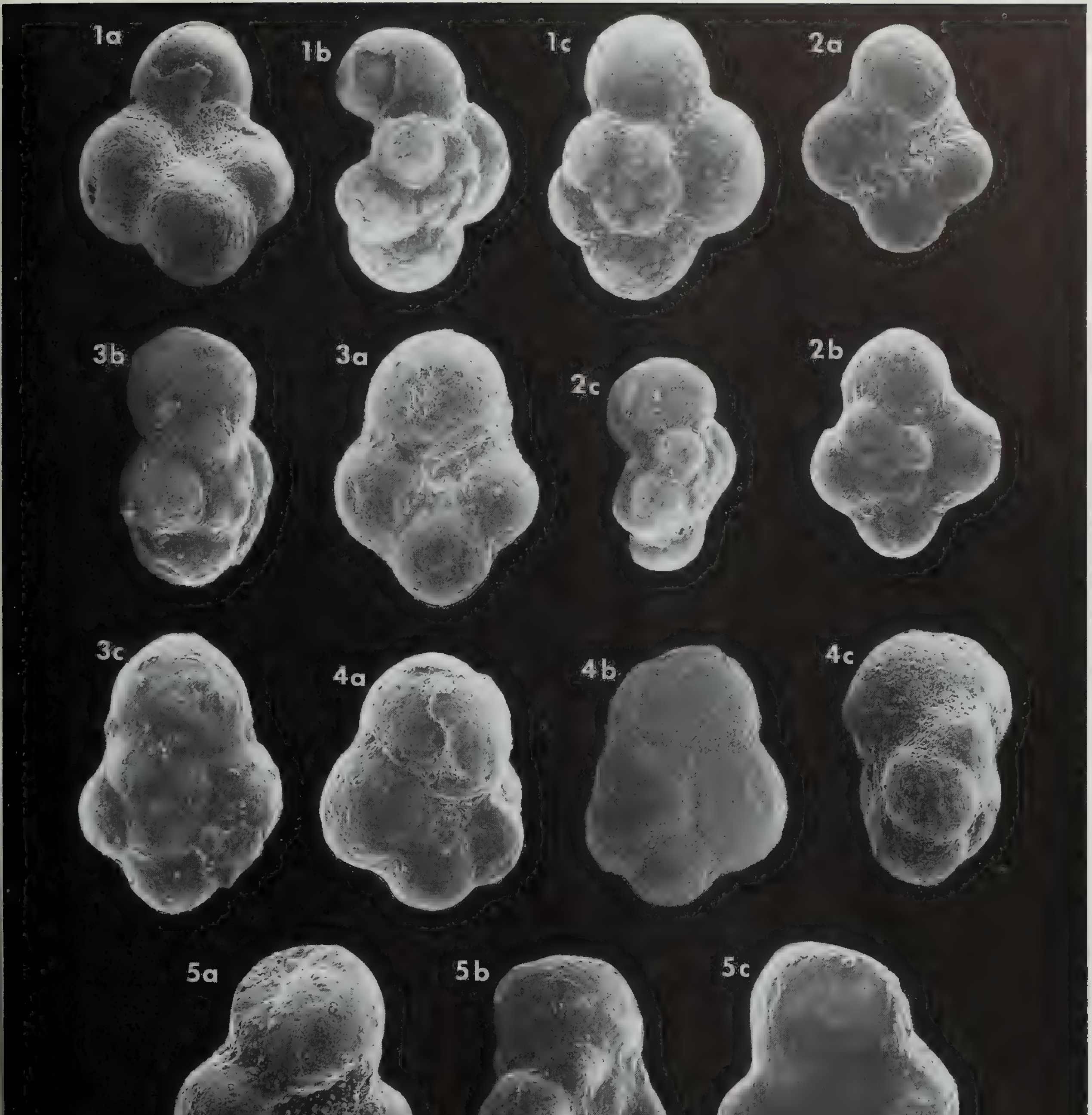


Plate 2

Fig.1 *Praehedbergella pseudosigali* n.sp. Late Barremian, Well 20/2–2, 8370 ft: a–c, ventral, peripheral and dorsal views of holotype, P52735, X 275.

ig. 2 *Praehedbergella sigali sigali* (Moullade). Early Barremian, Well 20/2–2, 8680 ft: a–c, ventral, dorsal and peripheral views, P52742, X 280.

ig. 3 *Praehedbergella sigali* (Moullade) *compacta* n.ssp. Early Barremian, Well 20/2–2, 8680 ft: a–c, ventral, peripheral and dorsal views, P52746, X 365.

ig. 4 *Praehedbergella tuschepsensis* (Antonova). Early Aptian, Well 16/28–6RE, 4150.5 m: a–c, ventral, dorsal and peripheral views, P52733, X 240.

ig. 5 *Praehedbergella* sp. cf. *P. handousi* (Salaj). Early Barremian, Well 20/2–2, 8680 ft: a–c, ventral, peripheral and dorsal views, P52734, X 350.

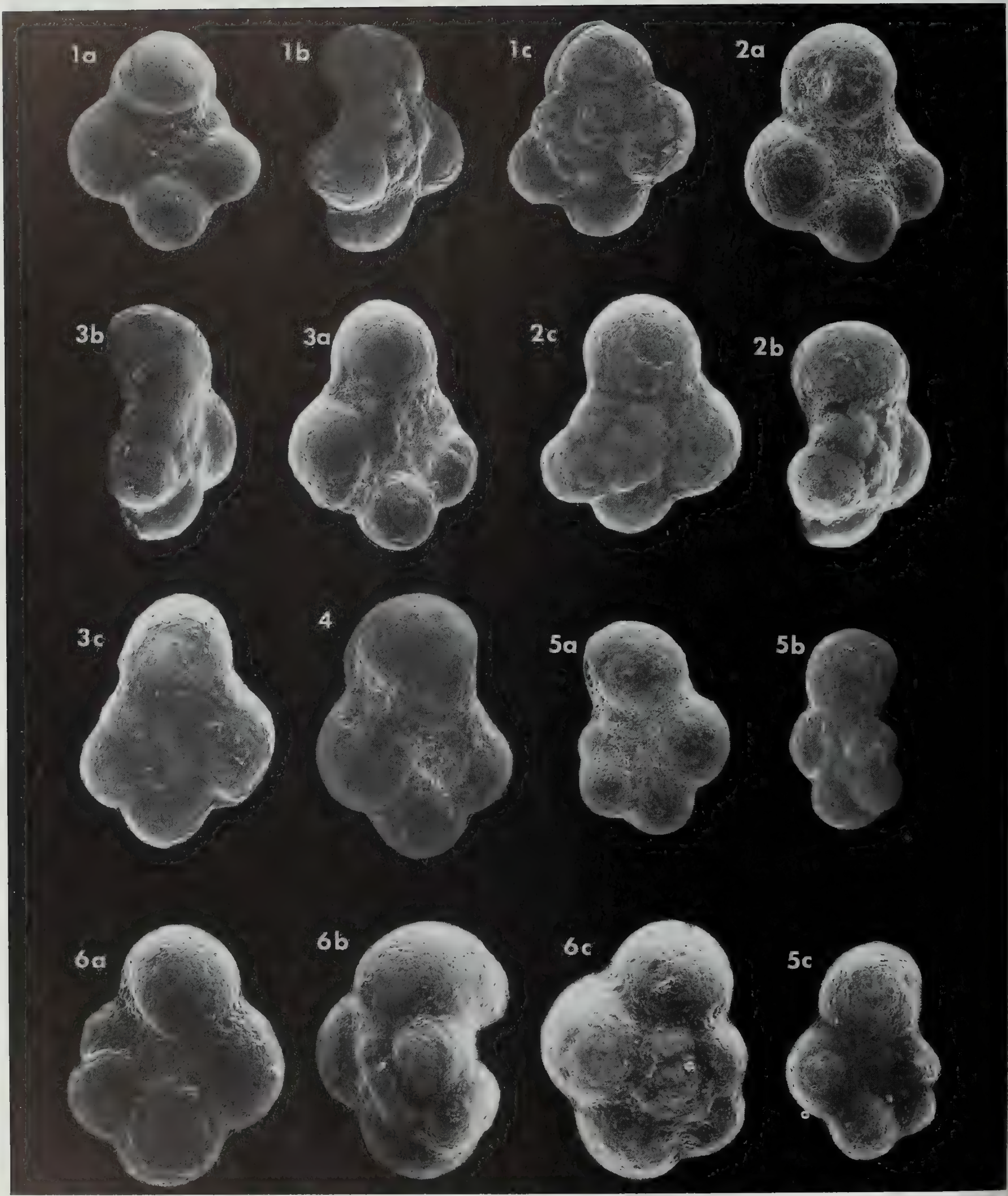
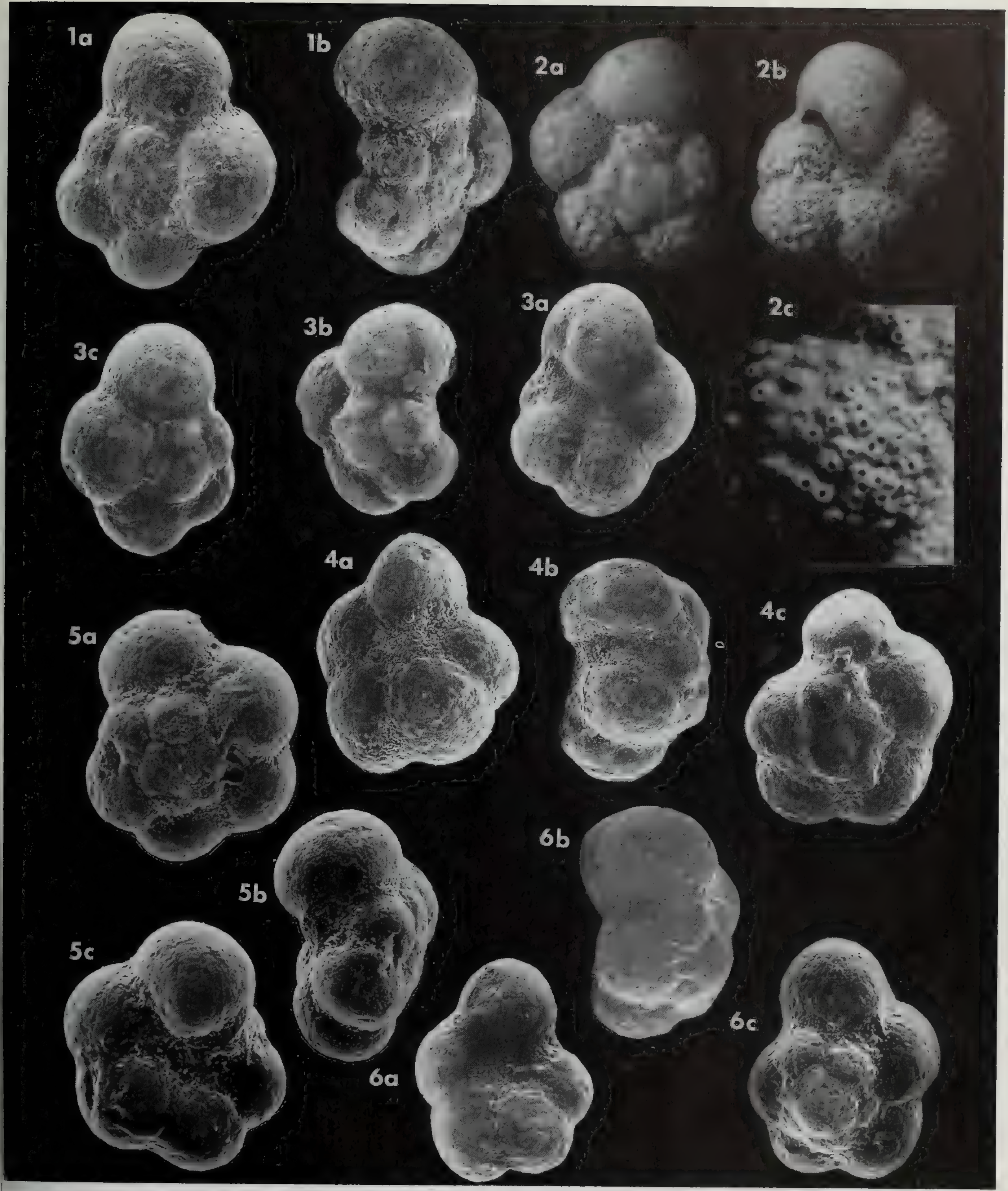


Plate 3

Figs 1–2 *Blefuscuiana laculata* n.sp. *sensu stricto*. Early Barremian, Well 20/2–2, 8680 m: 1a–c, ventral, peripheral and dorsal views of paratype P52725, X 210; 2a–c, ventral, peripheral and dorsal views of holotype, P52724, X 255.

Figs 3–5 *Blefuscuiana laculata alobata* n.subsp. Early Barremian, Well 20/2–2, 8680 m: 3a–c, ventral, peripheral and dorsal views of holotype, P52726, X 260; 4, ventral view of paratype P52728, X 250; 5a–c, ventral, peripheral and dorsal views of paratype P52727, X 250.

Fig. 6 *Blefuscuiana daminiae* n.sp. Early aptian, Well 15/30–3, 12830–40 ft: a–c, ventral, peripheral and dorsal views of holotype, P52696, X 220.



late 4

ig.1 *Blefuscuiana daminiae* n.sp. Early Aptian, Well 20/2–2, 8300 ft: a–b, dorsal and peripheral views of paratype, P52698, X 240.

ig. 2 *Blefuscuiana infracretacea* (Glaessner), probable metatype, collected by M.F. Glaessner in 1935, from R. Ubin, Ilkaya, North Caucasus, 'Albian'; U.S. National Museum of Natural History, no. 689757; a–b, dorsal and ventral views, X 230; c, perforation-cones on ventral side of second chamber of last whorl, x 690.

ig. 3 *Blefuscuiana daminiae* n.sp. Early Aptian: a–c, Well 15/30–3, 12830–40 ft. Ventral, peripheral and dorsal views of paratype, P52699 X 205.

igs 4–6 *Blefuscuiana infracretacea* (Glaessner) *aptica* (Agalarova). Early Aptian. 4a–c, Well 15/30–3, 12830–40 ft; ventral, peripheral and dorsal views of P52701, X 250. 5a–c, Well 20/2–2, 8300 ft; ventral, peripheral and dorsal views of P52702, X 215. 6a–c, Well 15/30–3, 12830–40 ft; ventral, peripheral and dorsal views of P52682, X 200.

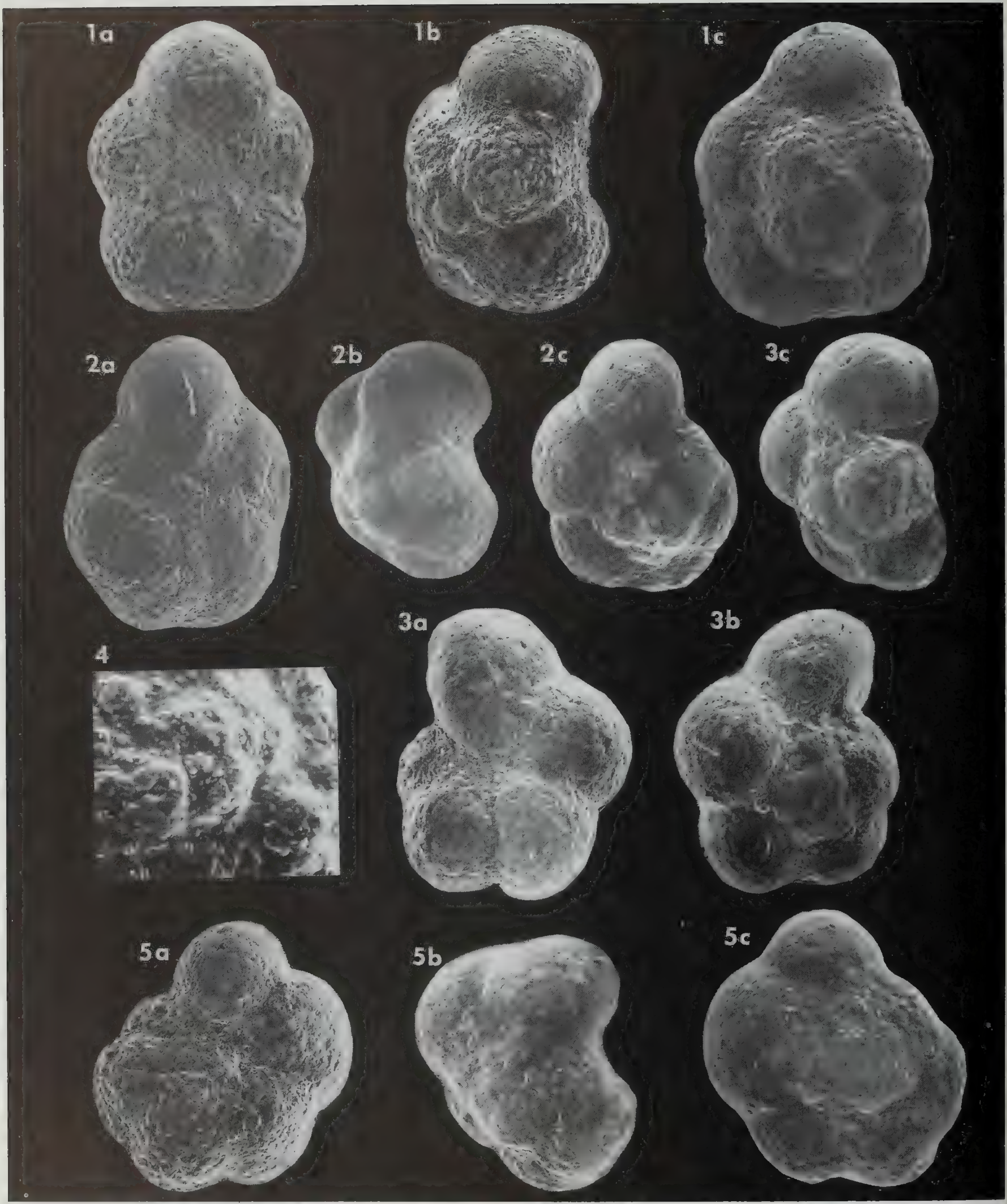


Plate 5

Fig.1 *Blefuscuiana rudis* n.sp. Early Barremian, Well 16/28–6RE, 4275 m; a–c, ventral, peripheral and dorsal views of holotype, P52713, x 200.

Fig. 2 *Blefuscuiana rudis* n.sp. Early Aptian, Well 20/2–2, 8250 ft; a–c, ventral, peripheral and dorsal views of paratype, P52715; a, x 430; b, c, x 360.

Figs 3–4 *Blefuscuiana whittakeri* n.sp. Early Aptian, Well 15/30–3, 12830–12840 ft; 3a–c, ventral, dorsal and peripheral views of holotype, P52717, x 290. 4, detail of perforation cones of holotype, x appr. 1160.

Fig. 5 *Blefuscuiana rudis* n.sp. Early Barremian, Well 16/28–6RE, 4195 m; ventral, peripheral and dorsal views of paratype, P52714, x 310.

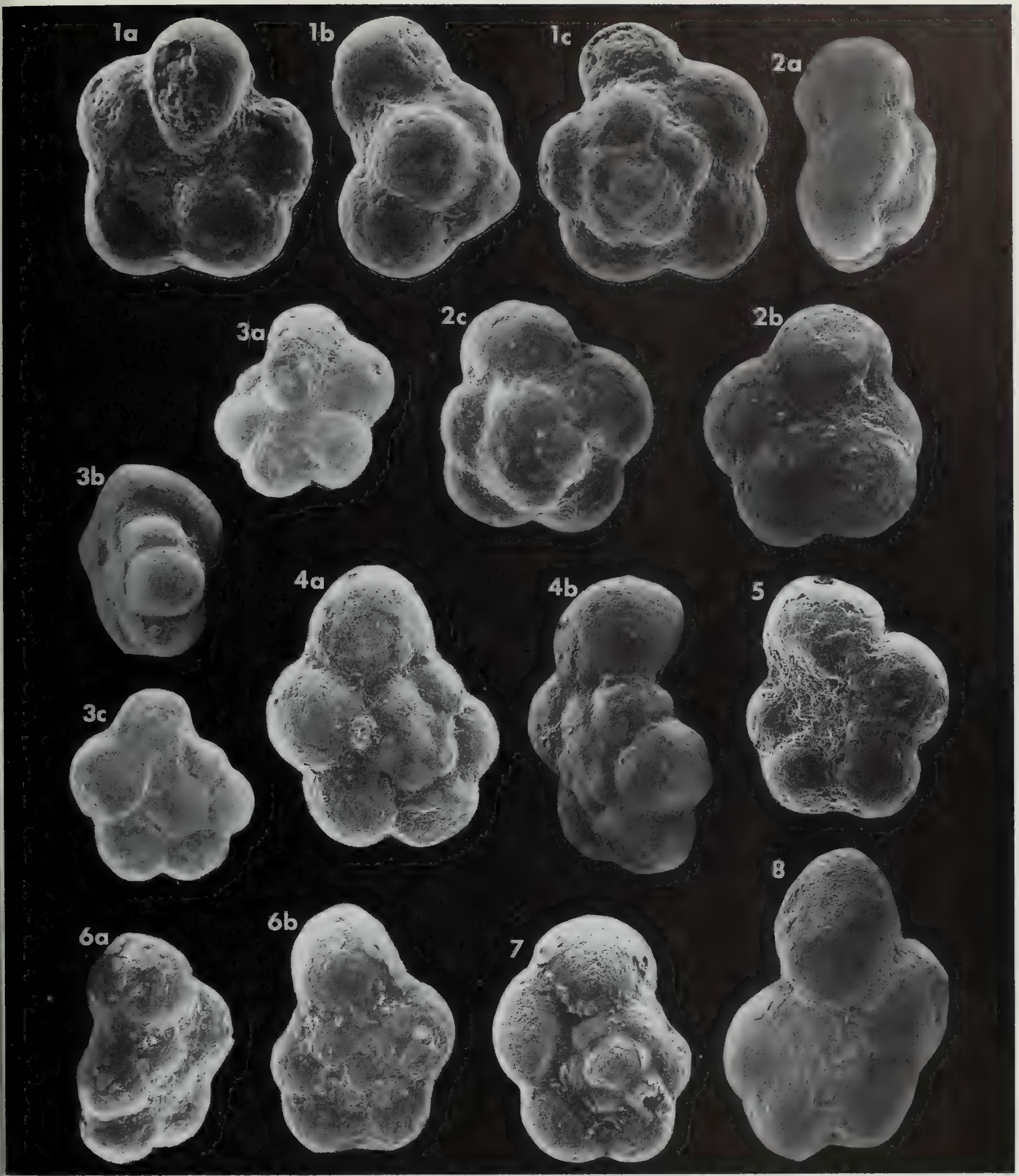


Plate 6

Figs 1–2 *Blefuscuiana excelsa* (Longoria) *cumulus* n.subsp. 1a–c, Early Aptian, Well 15/30–3, 12830–40 ft, ventral, peripheral and dorsal views of holotype, P52708, X 250. 2a–c, Early Aptian, Well 16/28–6RE, 4150.5 m, peripheral, ventral and dorsal views of paratype, P52709, X 240.

Fig. 3 *Blefuscuiana gorbachikae* (Longoria). Early Aptian, Well 16/28–6RE, 4150.5 m. Ventral, peripheral and dorsal views of P52687, X 170.

Figs 4–6 *Blefuscuiana aptiana aptiana* (Bartenstein). 4a–b, Early Aptian, Well 20/2–2, 8300 ft, dorsal and peripheral views of P52666, X 250. 5, Early Aptian, Well 16/28–6RE, 4178.5 m, ventral view of P52607, X 250. 6a–b, Early Aptian, Well 16/28–6RE, 4178.5 m, peripheral and dorsal views of P52665, X 325.

Fig. 7 *Blefuscuiana aptiana* (Bartenstein) *depressa* n.subsp. Early Aptian, Well 20/2–2, 8300 m. dorsal view of paratype P52712, X 250.

Fig. 8 *Lilliputianella eocretacea* (Neagu). Early Aptian, Well 16/28–6RE, 4160.7 m. Ventral view of P52732.

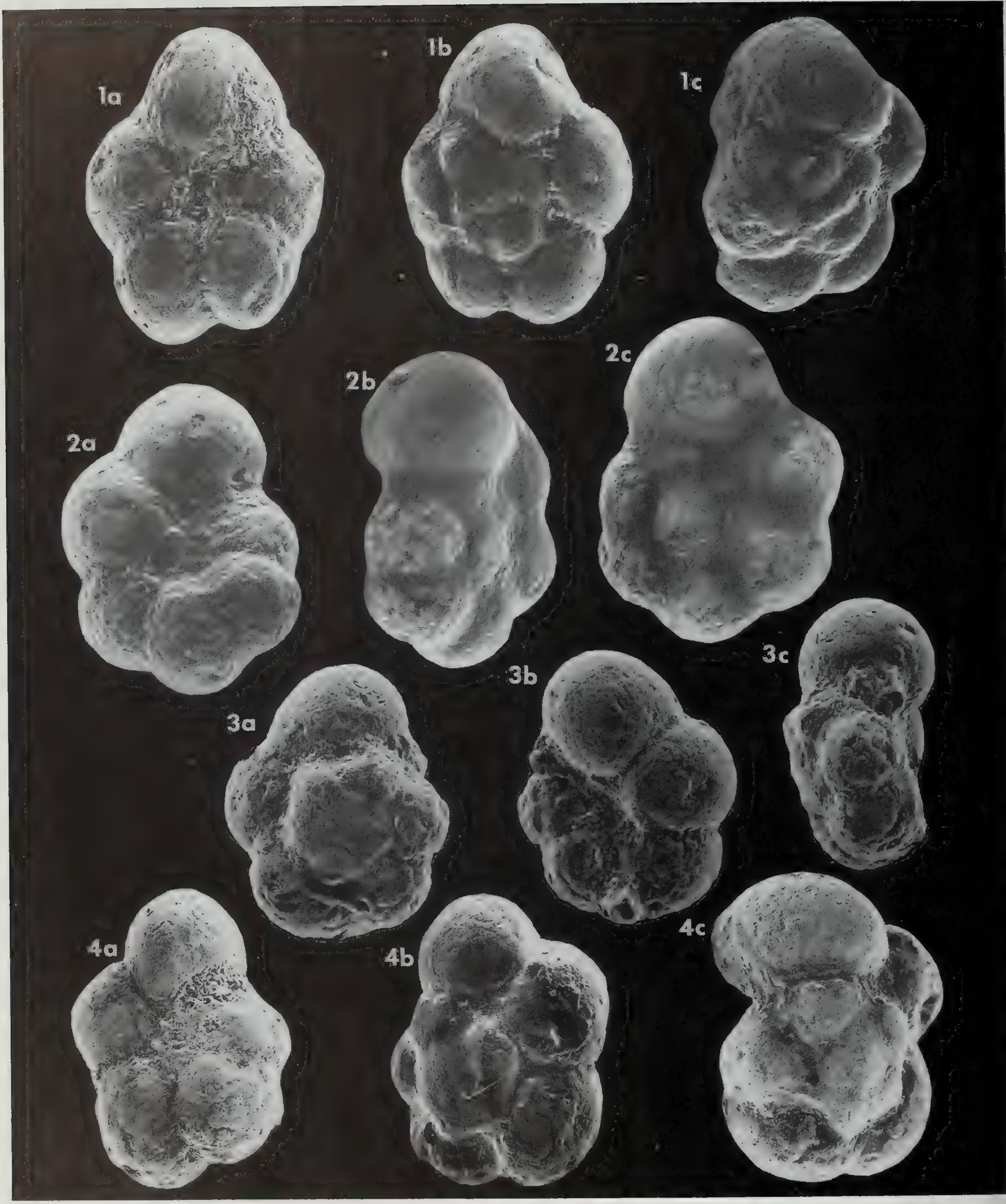


Plate 7

Fig.1 *Blefuscuiana aptiana* (Bartenstein) *depressa* n.subsp. Early Barremian, Well 16/28–6Re, 4260 m. a–c, ventral, peripheral and dorsal views of holotype, P52711, X 370.

Figs 2–4 *Blefuscuiana aptiana* (Bartenstein) *implana* n.subsp. 2a–c, Late Barremian, Well 20/2–2, 8370 ft, ventral, peripheral and dorsal views of paratype, P52707, X 250. 3a–b, Late Aptian, Well 20/2–2, 8210 ft, dorsal, ventral and peripheral views of holotype, P52705, X 260. 4a–b, Late Aptian, Well 20/2–2, 8210 ft, ventral, dorsal and peripheral views of paratype P52706, X 260.

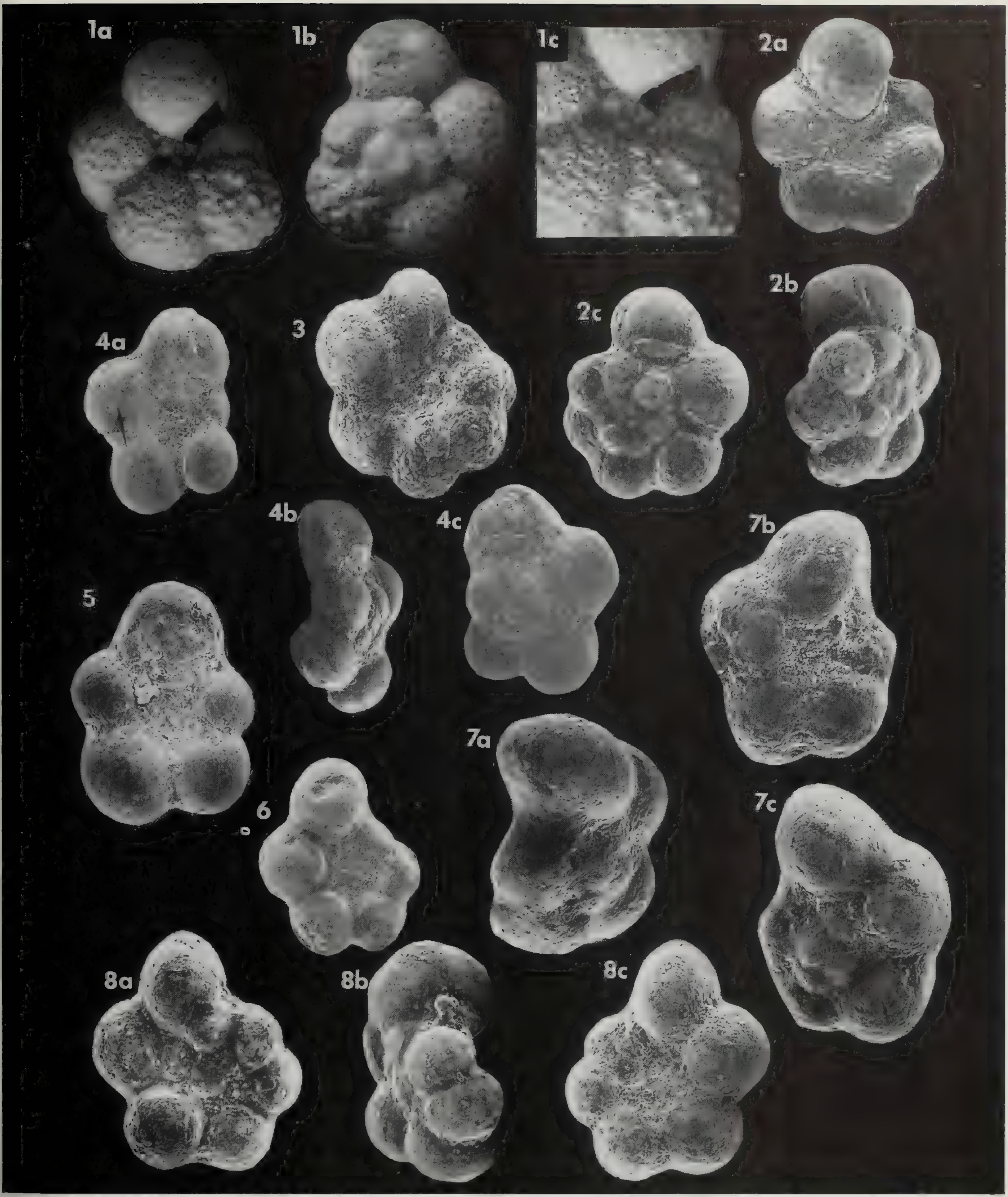


Plate 8

Fig. 1 *Blefuscuiana infracretacea* (Glaessner), probable metatype, collected by M.F. Glaessner in 1935, from R. Ubin, Ilkaya, North Caucasus, 'Albian'; U.S. National Museum of Natural History, slide no. 689757 (same slide as specimen figured Pl. 4, fig. 2); a, b, ventral and dorsal views, x 237; c, umbilical and apertural area, x 316.

Figs 2–3 *Blefuscuiana occulta* (Longoria) *perforocculta* n.ssp. Early Aptian, Well 20/2–2, 8300 ft. 2a–c, ventral, peripheral and dorsal views of holotype, P62677, X 175. 3, ventral view of paratype, P52678, X 180.

Figs 4–6 *Blefuscuiana praesimilis* n.sp. Early Barremian. 4a–c, Well 20/2–2, 8680 ft, ventral, peripheral and dorsal views of holotype, P52691, X 190. 5, Well 20/2–2, 8680 ft, ventral view of paratype, P52692, X 270; 6, Well 20/2–2, 8600 ft, ventral view of paratype, P52693, X 200.

Fig. 7 *Lilliputianella eocretacea* (Neagu). Early Aptian, Well 15/30–3, 12830–40 ft. Peripheral, ventral and dorsal views of P52731, X 230.

Fig. 8 *Lilliputianella similis* (Longoria). Early Aptian, Well 20/2–2, 8300 ft. Ventral, peripheral and dorsal views of P52730, X 210.

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Late Llandovery and early Wenlock stratigraphy and ecology in the Oslo Region, Norway

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SYNOPSIS. New fossil collections and field work in all parts of the Oslo Region in rocks of middle and late Llandovery and early Wenlock ages have led to a reassessment of the stratigraphical units, including the erection of a new Porsgrunn Formation of late Llandovery age in the Skien, Porsgrunn and Holmestrand districts. The fossils used for dating are reviewed in turn, with new graptolite records and new finds recorded of the age-diagnostic brachiopod *Eocoelia sulcata*. Many faunal assemblages and animal communities have been recognised, most of which are known from Britain, Canada and elsewhere. The new strophomenacean brachiopod genus *Erinostrophia* is erected, with type species *Orthis undata* M'Coy, 1846. Analysis of the deepening and shallowing of the animal communities, combined with a review of the sequence stratigraphy, leads to a recognition that, in addition to the variable influences of global eustatic changes, the more local isostatic responses to contemporary nappe emplacement were more important in controlling the depths and facies.

INTRODUCTION

The Silurian rocks of the Oslo Region are a challenge to biostratigraphers: they appear at first sight to be well exposed and very fossiliferous, but on closer inspection the exposure is discontinuous and the critical fossils for dating are often hard to find in many parts of the region. The rocks crop out sporadically over a large area over 220 km long from north to south and up to 80 km wide (Fig. 1), but in many places they have been metamorphosed by Permian intrusions; they are often intensely folded and faults are common. Even though they are in places exposed in sea or lake coastal sections it is often difficult to define lithostratigraphical boundaries and to measure complete sections with accuracy. Apart from crinoids and tabulate corals, which have not so far proved useful for dating, the fossils are often sparse or badly affected by cleavage or metamorphism, although they may sometimes be found excellently preserved, especially after careful preparation. The rocks of middle and later Llandovery and early Wenlock age form an important amount of the total Lower Palaeozoic sequence of the Oslo area and are the subject of this paper. To date this sequence it has been necessary to use a wide variety of fossils: graptolites, brachiopods, acritarchs, conodonts and even the button coral *Palaeocyclus*. In many cases these ages are not as precise as we would wish owing to the sporadic distribution of the fossils. We have also tried to evaluate the shifting patterns of the faunal distribution of macrofossils and to integrate these with the lithologies in order to understand something of the local environment and palaeobathymetry, which of course varied immensely in both time and space through such a substantial area.

The Oslo Region can be compared with coeval areas elsewhere, particularly the Welsh Borderland (Ziegler *et al.* 1968a), and one object of our studies has been to evaluate probable sea level changes and to compare them with areas in other palaeocontinents (McKerrow 1979, Johnson *et al* 1981, 1991), following preliminary work by Johnson & Worsley (1982).

The most substantial previous study of these rocks remains that by Kiaer (1908), who summarised earlier nineteenth century work by Brøgger, Kjerulf and others including Murchison. Kiaer divided the rocks by a number and letter system into 'Etagen' or 'Stages' from the Cambrian to the late Silurian, and most of the present paper deals with his stages 7 and 8. Worsley *et al* (1983) have provided a modern stratigraphical framework of formation names for the region and demonstrated some diachroneity in a few of Kiaer's subdivisions, the various authors in Worsley (1982) have published many new fossil identifications, and Baarli (1990) has published some useful ecological data on the Vik Formation in Malmøya (Oslo) and Sandvika (Asker). However, Kiaer remains the basic reference for many detailed sections over the area as a whole. The present paper concentrates on the later Llandovery of the area following work on the middle Llandovery (chiefly the Rytteråker Formation) by Möller (1987, 1989).

The various dating criteria will be reviewed first, followed by brief descriptions of the faunal assemblages which we have found, the details of the various formations and a geological history of the area.

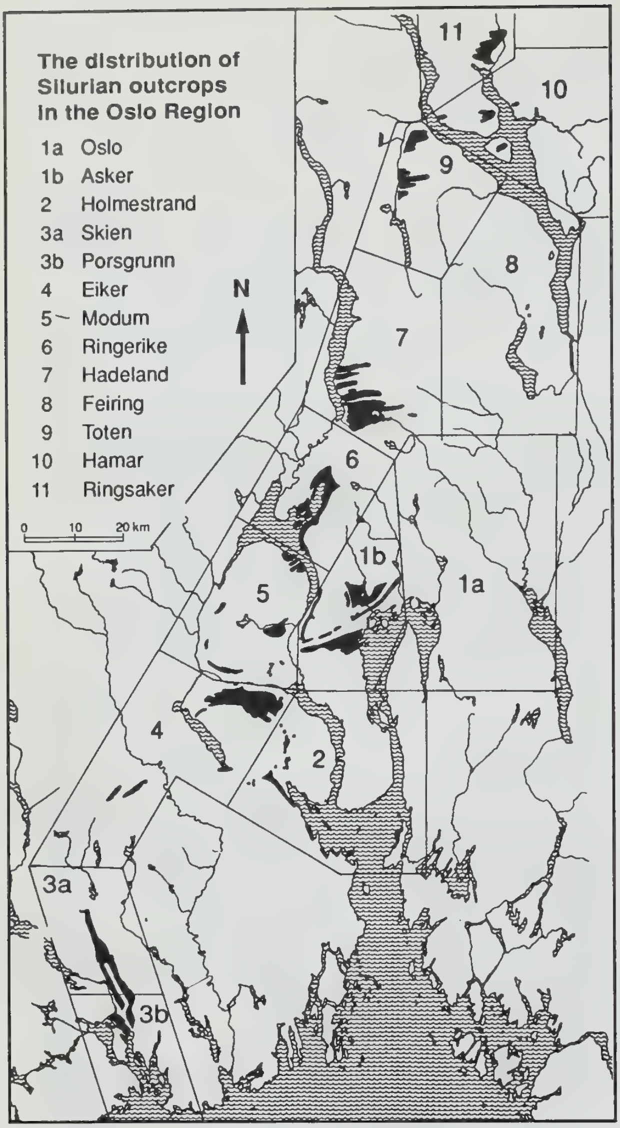

Fig. 1 Outcrop map of the Silurian of the Oslo Region, showing the districts mentioned in the text.

SHELLY CORRELATION ELEMENTS

Stricklandia–Costistricklandia

Since Williams (1951), this brachiopod lineage has afforded one of the best means of dating shelly rocks of Lower Silurian age. The earlier parts of the lineage are particularly well documented in the Oslo Region (Baarli 1986) and the later parts, those with *Stricklandia laevis* and *Costistricklandia lirata*, are also now known (Baarli & Johnson 1982, 1988). *S. laevis* has previously been recorded from the lower part of the Vik Formation in Asker, Malmøya and Modum and *C. lirata* from the upper Vik in Asker and the middle Vik and upper Bruflat in the Ringerike district. Baarli & Johnson (1988) also recorded and figured *Costistricklandia lirata* from the lower Vik Formation in the Skien district. However, the abundant stricklandiids which we have collected in the lower and middle Vik Formation in the Skien, Porsgrunn and Holmestrand districts (Fig. 7g–i) are identified here as *Stricklandia laevis* rather than *Costistricklandia lirata* since there are no substantial ribs and the cardinalia are also typical of that species. This change of identification from that of Baarli & Johnson makes a significant impact on the age deduced for the lower and middle Vik Formation of the southern parts of the Oslo region. We have also found *S. lens progressa* from the lower part of the Vik Formation in Asker. All these records have been instrumental in forming some of the most useful parameters for our correlation diagram of the area (Fig. 3).

Pentamerus–Pentameroides

Baarli & Johnson (1982, p. 96) have documented the transition between *Pentamerus oblongus* and *Pentameroides* cf. *subrectus* in beds 12 m above the base of the middle Garntangen member of the Vik Formation at Purkøya, Ringerike district and Baarli & Johnson (1988) added new records from Baerum. We have found *Pentameroides* to be abundant as low as 10 m above the base of the Vik Formation at Skien (Fig. 7j) and Porsgrunn and perhaps 20 m above the base at Holmestrand. These records are rather lower in the formation than expected, and probably indicate diachroneity of the lithologies.

Eocoelia

Since the classic work on the evolution of *Eocoelia* in the Llandovery by Ziegler (1966), the genus has been documented as also occurring in early Wenlock rocks by Bassett & Cocks (1974) as the species *E. angelini* (Lindstrøm). Although Kiaer (1908) described the lower part of the Llandovery sequence in Oslo as '6a, the zone with *Leptocoelia hemisphaerica*, Sow.', that common brachiopod has been shown (Thomsen & Baarli 1982, p. 64) to be a misidentification of the basal Silurian *Zygospiraella duboisi* (Verneuil). True *Eocoelia* has only been documented from the Oslo region below the Wenlock in a single record of *Eocoelia hemisphaerica* (Figs 7a–c) from the Rytteråker Formation of the Skien area (Baarli & Johnson 1988). Within rocks of Wenlock age, *Eocoelia angelini* has been found in the Braksøya Formation at Ringerike by Ziegler (1966 p. 538 — identified there as *E. sulcata*, but correctly re-identified by Bassett & Rickards 1971).

We have also found true *Eocoelia sulcata*, another new record for the Oslo Region (Fig. 7d), in the Porsgrunn Formation, 34 m below the contact with the overlying Braksøya Formation, at Kommersøya, Holmestrand district (Grid Ref. NL 750991), where it occurs with *crenulata* Zone graptolites. At the top of our sequence, the species *E. angelini* has been recorded from the Braksøya Formation at its type locality in the Ringerike district (Worsley *et al.* 1983, p. 35). These workers regard it as suggesting a mid-Sheinwoodian (*riccartonensis* Zone) age for that formation based on the co-occurrence with *riccartonensis* Zone graptolites in Gotland (Bassett & Cocks 1974). We have also found *E. sulcata* within 2 m of the base of the Malmøya Formation in the Baerum district at Daeliveien, (Locality 30, Grid Ref. NM 859428) and at Asterudveien (NM 869442). Locality 30 is in the same section and stratigraphically above Locality 27, which is Skinnerbukta Formation yielding *centrifugus* Zone age graptolites. This is a most important find, since it is the first certain

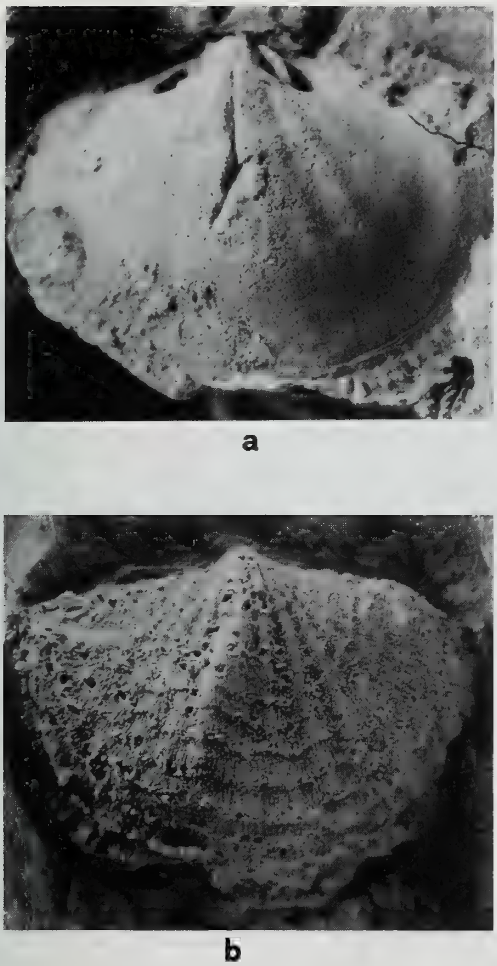

Fig. 2 *Eocoelia sulcata* (Prouty, 1923), from early Wenlock Malmøya Formation, Locality 30; 2a, internal mould of a pedicle valve, BC 10570, x 10; 2b, latex cast of the external mould of a pedicle valve, showing faint ribbing and frilly ornament, BC 10568, x 9.

record of *Eocoelia sulcata* (Fig. 2) from the Wenlock anywhere. Hitherto it has been assumed that *E. sulcata* evolved into *E. angelini* at about the Llandovery–Wenlock boundary, but now it seems clear that evolution took place within the *murchisoni* Zone.

Erinostrophia undata

In Appendix 1 below we erect the new generic name *Erinostrophia* for the large rugose brachiopod which has been known in the stratigraphical literature as *Strophomena walmstedti*, or *Megastrophia (Protomegastrophia) undata* or by almost any combination of these names. It is known from Gotland, Scotland and Ireland (Fig. 8a) as well as from Norway (Figs 8b–f), and it appears to be both a distinctive and easily recognizable form and also stratigraphically restricted to a narrow interval at the very top of the Telychian. There is no certain proof that it ever extended up into the Wenlock and it thus can be used as a sensitive age ndicator for rocks corresponding to the *crenulata* Zone.

Palaeocyclus

The small button coral *Palaeocyclus porpita* is well known from many late Llandovery localities, for example in Gotland, Wales, Scotland, Ireland and Canada (Gaspé), and it can often occur in very large numbers. In the Oslo Region, we have found it in the upper part of the Porsgrunn Formation, e.g. near Gjerpen Church, Skien (Grid Ref. NL 347654) and in the type section (Fig. 4) and in the lower part of the Braksøya Formation at Skien, Porsgrunn and Holmestrand. It is also common in parts of the Bruflat Formation in Ringerike and further north, for example in the railway section north of Jevnaker, Hadeland (NM 787825), although we have not found it in the Bruflat Formation of Toten. Although *Palaeocyclus porpita* is undoubtedly most abundant in rocks of *crenulata* Zone age, both in the Oslo Region and elsewhere, it is as yet unresolved whether or not this coral lingered on into earliest Wenlock time, but there is no hard evidence that it did. In the well-studied Vattenfallet section of Gotland, it is apparently confined to the Lower Visby Marl of late Llandovery age (Neuman & Hanken 1979) although there are other unconfirmed records of *Palaeocyclus* in the earliest Wenlock Upper Visby Marl.

OTHER CORRELATION ELEMENTS

Graptolites

Graptolites are relatively scarce in the Oslo Region, apart from the common assemblages in the Ek Formation of Toten and Ringsaker and the basal Skinnerbukta beds at Malmøya (Howe 1982), although there are a few other records of occasional specimens in Kiaer (1908) and Bassett & Rickards (1971). We have collected graptolites from several new localities which have proved crucial to our correlation, particularly of the Porsgrunn and Skinnerbukta formations. These have been identified for us by Dr R.B. Rickards, and consist of the following:–

Porsgrunn Formation: Locality 2 — *Monograptus priodon/ ?M. parapriodon* — indicating *crenulata* Zone age. Locality 3 — *Monoclimacis* (long); cyrtograptid arm.

Bruflat Formation: Locality 14 — *Monograptus* sensu stricto — uncertain age.

Skinnerbukta Formation: Locality 26 — *Monoclimacis vomerina vomerina*; *M. v.* aff. *basilica, Monograptus* cf. *priodon* — together indicating *centrifugus* or low *murchisoni* Zone age. Locality 27 — *Retiolites geinitzianus angustrifrons; Pristiograptus* cf. *watneyae* — probably indicating *centrifugus* Zone age. Locality 33 — *Monograptus priodon; Monoclimacis vomerina basilica* — indicating *centrifugus* or low *murchisoni* Zone age.

Microfossils

New studies on conodonts from the Vik Formation at Malmøya, Oslo, and at Sandvika, Baerum, and the Rytteråker Formation at Malmøykalven, Oslo, have been made by Nakrem (1986). Aldridge & Mohamed (1982) have also figured some conodonts from the Bruflat Formation of Ringerike, the Vik Formation of Holmestrand and Asker and from what we would now term the Porsgrunn Formation of Skien. These studies have recognised *celloni* Zone faunas

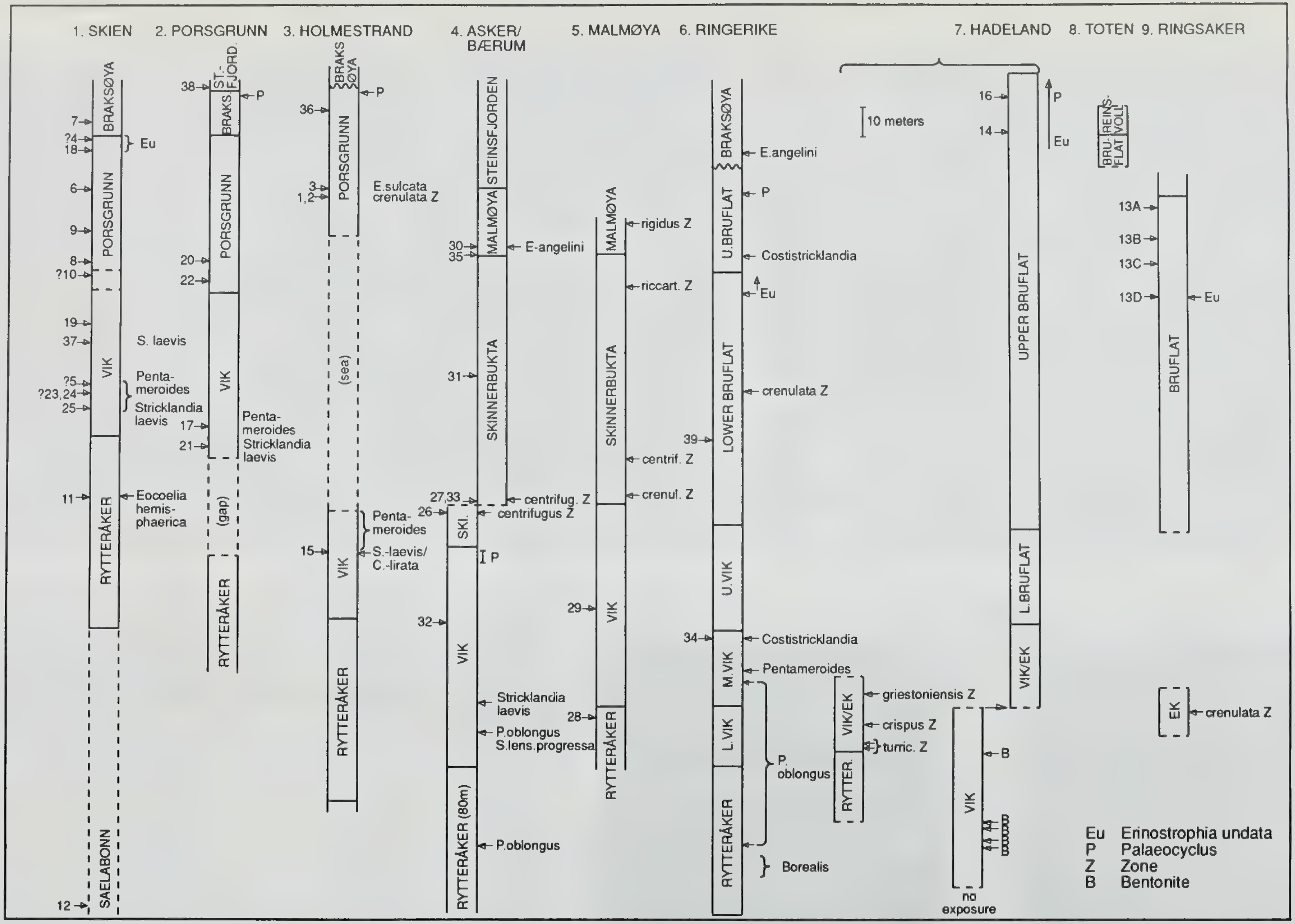
1. SKIEN
2. PORSGRUNN
3. HOLMESTRAND
4. ASKER/ BÆRUM
5. MALMØYA
6. RINGERIKE
7. HADELAND
8. TOTEN
9. RINGSAKER
BRAKSØYA
PORSGRUNN
VIK
RYTTERÅKER
SAELABONN
7
?4
18
6
9
8
?10
19
37
?5
?23,24
25
11
12
Eu
S. laevis
Penta-meroides
Stricklandia laevis
Eocoelia hemis-phaerica
ST.-FJORD.
BRAKS
(gap)
38
20
22
17
21
P
Penta-meroides Stricklandia laevis
BRAKSØYA
(sea)
36
3
1,2
15
E.sulcata crenulata Z
Penta-meroides
S.-laevis/ C.-lirata
STEINSFJORDEN
MALMØYA
SKINNERBUKTA
SKI.
RYTTERÅKER (80m)
30
35
31
27,33
26
32
E-angelini
centrifug. Z
centrifugus Z
Stricklandia laevis
P.oblongus
S.lens.progressa
P.oblongus
29
28
rigidus Z
riccart. Z
centrif. Z
crenul. Z
U.BRUFLAT
LOWER BRUFLAT
U.VIK
M.VIK
L.VIK
39
34
E.angelini
Costistricklandia
crenulata Z
Pentameroides
P. oblongus
Borealis
10 meters
VIK/EK
RYTTER.
griestoniensis Z
crispus Z
turric. Z
UPPER BRUFLAT
L.BRUFLAT
16
14
B
no exposure
BRU-FLAT
REINS-VOLL
BRUFLAT
EK
13A
13B
13C
13D
Eu Erinostrophia undata
P Palaeocyclus
Z Zone
B Bentonite

Fig. 3 Composite sections through selected late Llandovery and early Wenlock rocks of the Oslo Region, (vertical scale thickness). The key new occurrences of graptolites and brachiopods essential for correlation are shown on the right of the columns, and the locality numbers on the left. 1, Skien: composite section from Kapitalberget (NL 357629) and at Hesthagveien (NL 357625); 2, Porsgrunn: measured section at Øyekastvegen road cuttings (NL 367456 to NL 370555); 3, Holmestrand: measured coastal sections on Killingsholmen (around NL 752995) and Kommersøya (NL 750991 to NL 748991); 4, Asker/Baerum: upper part from road exposures near Daeliveien (around NM 859428) and temporary exposure near Øverland (NM 871444); lower part near Kampebraten, Sandvika (around NM 846404); 5, Malmøya: measured section from Malmøykalven (around NM 976377) to Skinnerbukta hill (NM 985385) — there are additional records for sections 4 and 5 in Baarli (1990); 6, Ringerike: composite section measured by D. Alm; 7, Hadeland: to left, measured section at Storskjaeringa railway cutting (NM 843851); to right (lower), measured section at roadside N of Jevnaker (around NM 781828); (upper) measured section at railway cuttings 3km N of Jevnaker (NM 787822 to NM 787825); 8, Toten: measured exposure by road at NN 876270; 9, Hamar: measured section at Reinsvoll railway cutting (NM 881269).

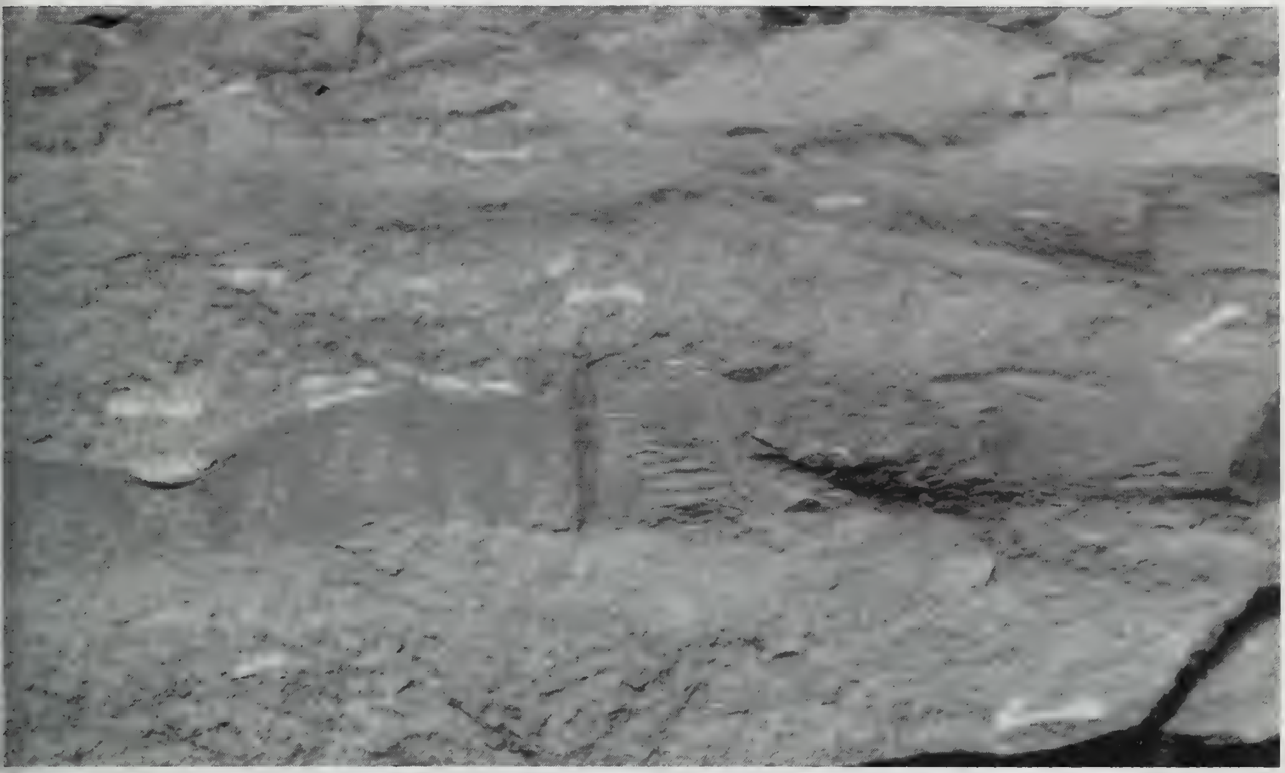

Fig. 4 Upper part of Porsgrunn Formation at Øyekastvegen, Porsgrunn (NL 370555), showing interbedded bioclastic siltstones and limestones with cross sections through the button coral *Palaeocyclus porpita* (diameter of each coral is approximately 1 cm).

from the lower part of the Vik Formation and *amorphognathoides* Zone faunas from the upper Vik, lower Skinnerbukta and middle Bruflat Formations. Palynomorphs have been studied in the Ringerike District by Smelror (1987) who has recognised the zones erected by Hill (1974; revised Hill & Dorning *in* Cocks et al. 1984) in the Welsh Borderland and the type Llandovery area in Wales. Smelror recognised the Zone 3 — Zone 4 boundary two-thirds way up the Vik Formation at Ringerike and the Zone 4 — Zone 5 boundary near the top of the Bruflat Formation. Although most of these micropalaeontological data are less precise than those from the graptolites and shelly fauna, they are useful confirmatory evidence in correlation.

FAUNAL ASSEMBLAGES

Although Kiaer (1908) listed a great many species from late Llandovery and early Wenlock beds from many localities in the Oslo Region, closer inspection of these lists shows that very few of the species names are known from coeval beds elsewhere. Most of the names are generalised from, for example, Davidson's brachiopod monograph from the Wenock of Britain (Davidson 1866–71). In fact, there has been ittle systematic palaeontological work done on the late Llandovery or early Wenlock brachiopods of the Oslo Region, apart from that on the strophomenids by Holtedahl 1916), a few illustrations in a preliminary survey by Cocks & Baarli (1982) and a description of the enteletaceans by Baarli (1988). Monographic revisions of the fauna would be desirable, although the potential task of assembling truly adequate collections is daunting. However, we have collected systematically from 35 localities (Tables 1,2) yielding over 5000 specimens in the Palaeontologisk Museum, Oslo (PMO) and The Natural History Museum, London (BB,BC). In addition, we have observed many comparable fossil assemblages in the field without making detailed collections, and Baarli (1990) has identified 302 fossils from 7 collections in the Vik Formation of Malmøya, Oslo, and 567 specimens from 5 collections in a section in the Vik Formation at Kampebråten, Sandvika (area 1b on our Fig 1).

Many of the assemblages present may be assigned to those previously recognized from the late Llandovery of the Welsh Borderland (Ziegler *et al.* 1968a, Cocks & McKerrow 1984) and elsewhere, namely the *Eocoelia, Pentamerus*/*Pentameroides, Stricklandia* and *Clorinda* Communities (Fig. 6). However, in the Oslo Region these assemblages are supplemented by bioherms, shallow-water molluscan dominated assemblages and two other assemblages, the *Atrypa*–*Hallopora* Community of the mid-shelf and the *Eoplectodonta–Atrypa* Community of the deeper shelf, upon which brief notes follow. As with the Welsh Borderland (Ziegler *et al.* 1968b) the presence of these assemblages has assisted in the recognition of deepening and shallowing trends in the various formations, which are reviewed later.

Table 1 Fossils recovered from various localities in the Vik Formation. The localities are given in Appendix 2.

Locality Number	17	23	24	25	5	21	34	19	29
Craniops									2
Orbiculoidea									1
Dictyonella	3								
Hesperorthis							1		
Skenidioides	8	4			3				15
Indet. orthid	1								
Isorthis	2	16		2		1			19
Dalejina								1	
Resserella								1	1
Visbyella				1					
Dicoelosia								2	47
Eoplectodonta	1							5	21
Aegiria					11				
Katastrophomena									1
Leptostrophia			1						
Brachyprion	13	4							
Mesopholidostrophia				1	1				
Protochonetes	3								
Pentameroides	99	79	96	45					
Stricklandia	3	3	1	32	38	23	16		
Clorinda	59	31	7	16	2	5			
Parastrophinella	1								
Atrypa	13	23	4	145	178			9	14
Atrypina									1
Hyattidina		1							
Glassia	2	6							
Pentlandella	17								
Eospirifer					14			4	
Cyrtia									15
Tabulate corals	24	48	9	7	21	1			
Rugose corals	23	16		2	4			2	3
Bryozoa	10	12	4		28	1	7	23	34
Molluscs		1			2			3	6
Ostracods								3	
Trilobites				1	1	1		2	10
Crinoids	2	7	3		2		1	32	115
Others	2	3		11	6			2	2
Total	285	254	125	263	309	32	25	90	307
Total species	26	21	11	15	17	6	5	18	28

Shallow-water

Bioherms

These are best developed in the early Wenlock Braksøya Formation, and extend from Porsgrunn northwards as far as Ringerike. They have not been collected and examined closely in the present study but are briefly described in Worsley *et al.* 1983, pp. 33–36.

Mollusc dominated assemblages

At the top of the Bruflat Formation, for example in the railway cutting south of Reinsvoll (Grid Ref. NN 881269), some bedding planes are covered with a variety of molluscs, dominantly gastropods. Our collection (Locality 13) has had the following molluscs identified by Dr N.J. Morris: Gastropods:– *Oriostoma* cf. *acuta* Lindström (80 specimens and 20 operculae), *Loxonema* sp. (46), *Gyronema*? sp. (42), *Raphistomina* sp. (19), and *Crespedostomus* sp. (1). Bivalves:– *Pteronitella* sp. (19), *Praenucula* sp. (7), *Koenenia*? sp. (1), ?grammysiid (1) and cyrtodontid (1); as well as a michelinoceratid cephalopod (6). The rest of the collection consisted of the brachiopods *Erinostrophia undata* (6 pedicle valves, 3 brachial valves), *Isorthis* sp. (4,3) and a single pedicle valve each of *Pentlandina* sp., *Atrypa* sp. and *Atrypina?* sp., 8 bryozoans, the trilobites *Dalmanites* (1), a calymenid (4), and a lichid (1); *Cornulites* (1), *Tentaculites* (5) and a few disarticulated crinoid columnals, making a total of 223 molluscs out of a collection of 269 specimens, or 83%. These occurrences, although not identical to any found in the Welsh Borderland, are comparable to the assemblages found in beds of approximately the same age in south-east Dyfed (Pembrokeshire), Wales (Walmsley & Bassett 1976).

Eocoelia Community

An interbed of shale within the limestones of the Rytteråker Formation at a road cut in Skien (Locality 11, Grid Ref. NL 336657) yielded a small fauna consisting of *Protatrypa* (18 pedicle valves, 9 brachial valves), *Eocoelia hemisphaerica* (J. de C. Sowerby) (4,11), *Pentamerus* (4,5), *Stricklandia* (1p.v.), *Clorinda* (1p.v), and 9 pieces of crinoid columnals. The *Eocoelia hemisphaerica* is of particular interest (Fig. 7a–c), since it is the first record of the species from the Oslo Region (Baarli & Johnson 1988). Although specimens of

Table 2 Fossils recovered from various localities in the Porsgrunn (P), Skinnerbukta (S) and Bruflat (B) Formations. The localities are given in Appendix 2.

Locality Number	P 36	P 22	P 20	P 8	P 1	P 4	P 18	P 6	P 2	P 3	P 9	P 10	S 31	S 35	B 14	B 16	B 39
Craniops	2		1	3				1		2	1	2					1
Dinobolus		1															
Petrocrania													1				
Orbiculoidea		2							1								
Philhedra			1														0
Skenidioides	9	4	3	3				1	1								
Indet. orthid									1	1							
Isorthis	9	40	13	3		2	2	51			10		3	63	3	14	5
Salopina							2			5		1					
Dalejina	5				1				5	6							
Resserella			1	5					4	20		9					3
Dicoelosia	7	14	9	2								1				1	
Triplesia									1								
Leangella											1						
Eoplectodonta	21	33	27	18	1	1			1	8	9	5	1				19
Jonesea		1															
Leptaena	3	7		1	1			1	4	6			5			5	7
Pentlandina			3														
Cyphomenoidea								1				1					1
Katastrophomena	4								1	7							1
Leptostrophia										2							
Strophonella			1														
Protomegastrophia				1	1				2	2							
Erinostrophia				12			2								73	10	
Amphistrophia		1		1							1						
Mesopholidostrophia					1		3					1					
Coolinia	10	1	2		1		1			2			2				3
Protochonetes	4			4		2	40	1		3	1		1	2		16	
Clorinda		2															
Eocoelia										3				81			
Rostricellula							1										
Sphaerirhynchia				2		3	4				8					4	
Rhynchonellid										1					1	1	
Atrypa	11	30	38	27			3	7	73	14	35	9	6		68	14	22
Atrypina		10					2									5	
Hyattidina						7	115									23	
Glassia		2	2	3							1	1					1
Homoeospira				10							1		1				
Eospirifer	3		1						2		1						
Cyrtia	17	7	10	2	1					1	6	1					4
Howellella									3	3	1						
Indet. brachiopods								1									
Tabulate corals	5			5			6		2		1				3	10	
Rugose corals	7	16				17	6		3		2	2			5	12	1
Bryozoa	53	10	17	12	6	13	56	23	34	141	18	10	18	67	80	113	6
Molluscs	1	6	24	2		6	4	1	3	8	5	2		1	4	58	2
Ostracods		3	24	62		4		5		11	7	9	1	19		8	
Trilobites	14	16	12	6	2	1	3	7	6	6	2	8	4	2	2	2	5
Crinoids	9	12	20	14		17	40	7	4	4	17	7	1	2	7	134	
Others	14	1	8	5	3	3	5	5	3	10	2		2	24	3	3	
Total	209	219	221	189	19	88	295	112	153	268	123	69	46	261	239	423	81
Total species	27	28	30	27	14	17	25	21	26	31	26	21	15	9	18	30	17

Eocoelia sulcata have been found in the Porsgrunn Formation (Fig. 7d), another new record, the assemblage in which they occur (Locality 3), is dominated by *Atrypa* and *Resserella* (Table 1) and represents a mid to deeper shelf community. The next *Eocoelia* community assemblage is to be found near the base of the Malmøya Formation (Fig. 2), for example at a roadside exposure at Daeliveien, Baerum, (Locality 30: Grid Ref. NM 859428) which yielded *Eocoelia sulcata* (124 pedicle valves, 94 brachial valves), *Isorthis*? sp. (44,29), *Protochonetes* (24,9), *Coolinia* (3,7), *Stegerhynchus* (4,5), *Cryptothyrella* (4,3), and single valves of *Eoplectodonta, Erinostrophia undata* and *Atrypa*, as well as 53 bryozoans, a gastropod, *Pteronitella* (3), *Harpidella* (3), *Tentaculites* (27), 12 ostracods and a single crinoid ossicle.

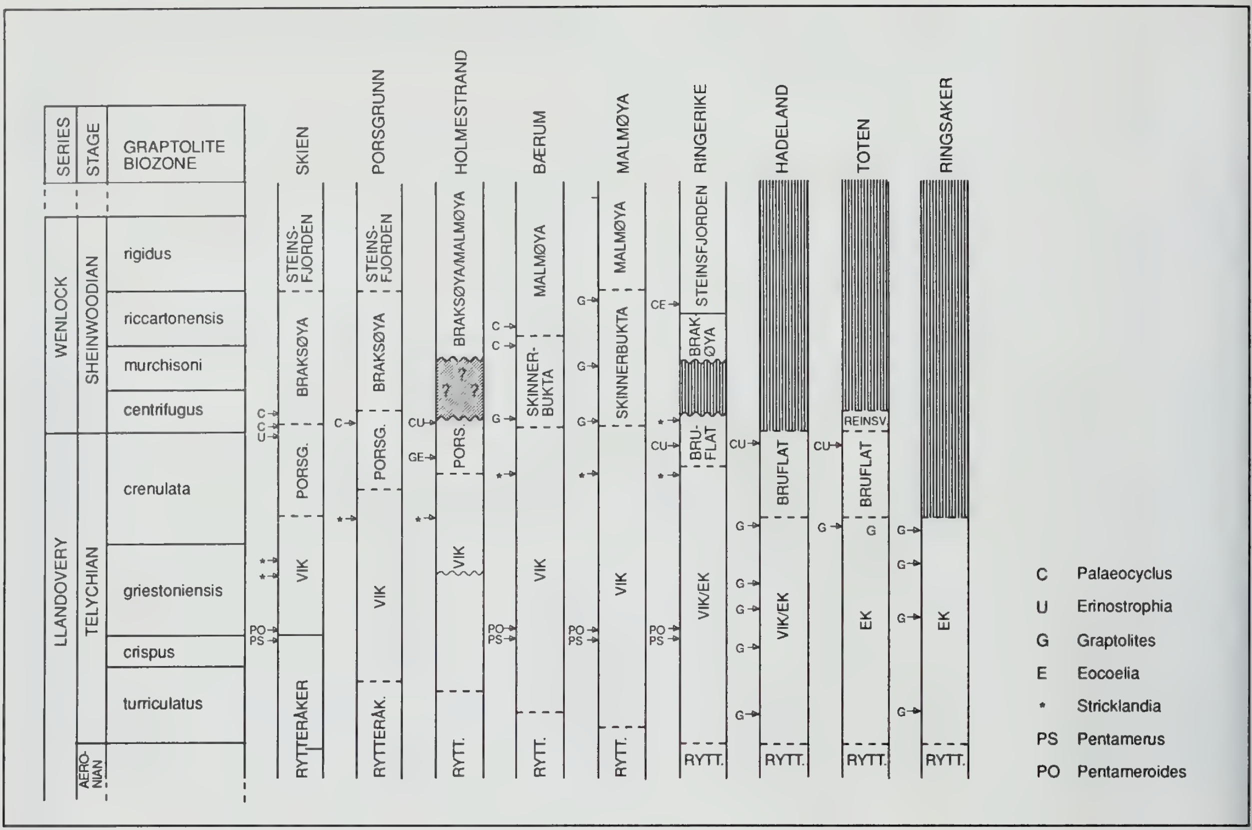
SERIES
STAGE
GRAPTOLITE BIOZONE
WENLOCK
SHEINWOODIAN
LLANDOVERY
TELYCHIAN
AERONIAN
rigidus
riccartonensis
murchisoni
centrifugus
crenulata
griestoniensis
crispus
turriculatus
SKIEN
PORSGRUNN
HOLMESTRAND
BÆRUM
MALMØYA
RINGERIKE
HADELAND
TOTEN
RINGSAKER
STEINS-FJORDEN
BRAKSØYA
PORSG.
VIK
RYTTERÅKER
RYTTERÅK.
BRAKSØYA/MALMØYA
PORS.
RYTT.
MALMØYA
SKINNER-BUKTA
SKINNERBUKTA
STEINSFJORDEN
BRAK-ØYA
BRU-FLAT
VIK/EK
BRUFLAT
REINSV.
EK
C Palaeocyclus
U Erinostrophia
G Graptolites
E Eocoelia
* Stricklandia
PS Pentamerus
PO Pentameroides

Fig. 5 Composite sections through selected late Llandovery and early Wenlock rocks of the Oslo Region. The vertical scale shows time.

Mid-shelf

Atrypa–Hallopora Community

This community recurs in the Vik, Porsgrunn and Bruflat formations, and is dominated by the brachiopod *Atrypa* and the bryozoan *Hallopora*. Good collections have been obtained from the Porsgrunn Formation at Holmestrand (Localities 2,3) and at Skien (Localities 9,10) where between 21 and 31 different species have been recorded (Table 2), including in Locality 3, *Eocoelia sulcata* (Fig. 7d). Both the faunal diversity and the general lithostratigraphical situations suggest that this fauna lived in the mid-shelf; although in the Bruflat Formation in Hadeland the main elements of the community are joined by dominant *Erinostrophia* (Locality 14) and other elements which are known from shallower water such as *Protochonetes* and *Hyattidina* (Locality 16), all suggesting the shallower part of the middle shelf.

Stricklandia and *Pentameroides* Communities

These assemblages are well known from many parts of the world, following their original description from the Welsh Borderland (Ziegler *et al.* 1968a), and are common in the Oslo Region. In particular we have many new records from the Vik Formation (Table 1) of the southern part of the region (Fig. 7j), particularly in the Skien (Localities 5,23–25) and Porsgrunn (Localities 17,21) districts, and a representative sample from Ringerike (Fig. 7i, Locality 34) from which these communities are already recorded (Baarli & Johnson 1988). Baarli (1990) has also recorded them from the Vik Formation of Sandvika and Malmøya.

Deeper-shelf

Eoplectodonta–Atrypa Community

This community has a comparable ecological position to the *Clorinda* Community (see below), however, *Clorinda* itself is absent (apart from 2 specimens from Locality 22). It is known from the Porsgrunn Formation at Holmestrand (Locality 1), Skien (Locality 8) and Porsgrunn (Localities 20,22) and from the Vik Formation at Skien (Locality 19) and Malmøya (Locality 29). Its diversity is fairly high, and it includes such forms as *Dicoelosia* and rare *Jonesea* (a common plectambonitacean formerly recorded from many places under the name of *Aegiria grayi*) which are only known elsewhere from outer shelf deeper-water deposits.

Clorinda Community

At only one place (Locality 32), in the Vik Formation at Baerum, have we collected a sparse but typical *Clorinda* Community consisting of 7 specimens of *Clorinda globosa*, one each of *Eoplectodonta penkillensis* and *Atrypa* and a mere two small ostracods. Elsewhere in the late Llandovery of the Oslo Region *Clorinda* only occurs commonly in the storm-deposited sandstones of the Vik Formation at Skien and Porsgrunn (e.g. Localities 17,23) and also in the base of

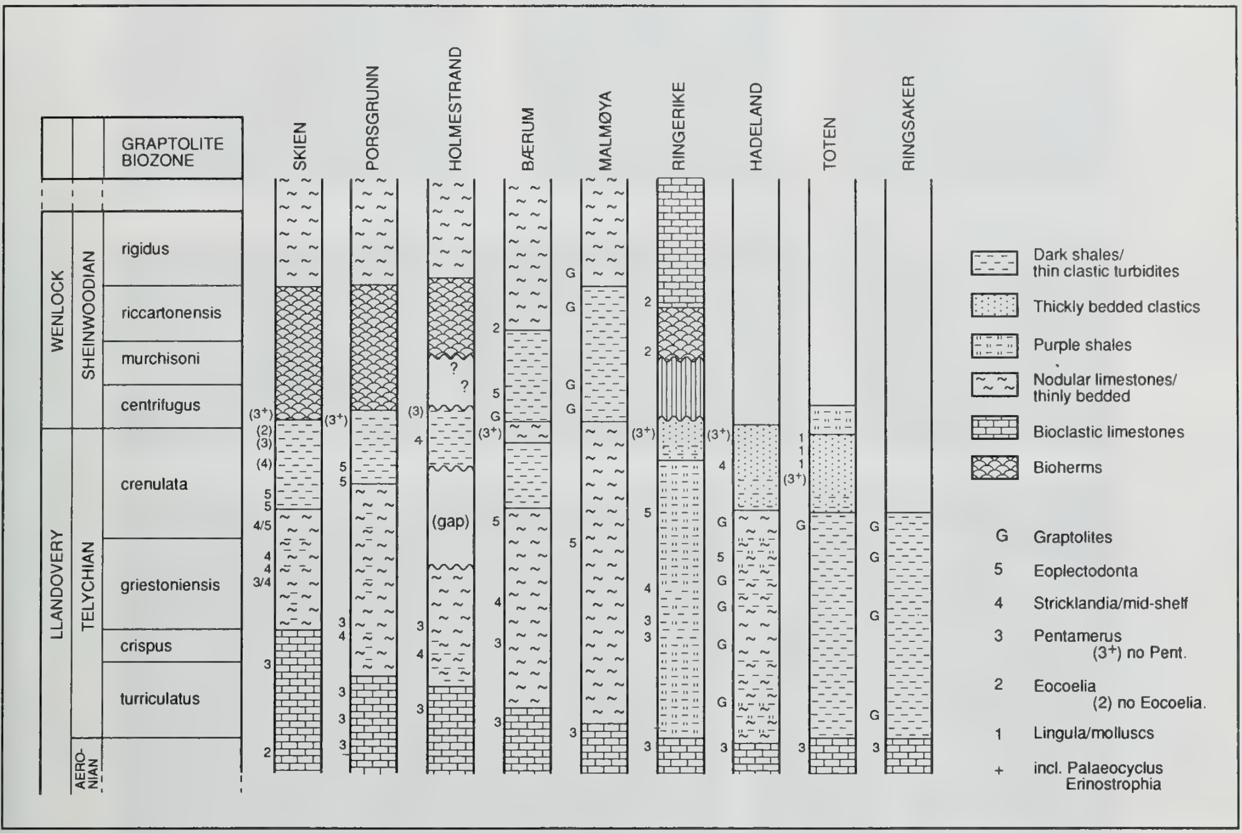
GRAPTOLITE BIOZONE
WENLOCK
SHEINWOODIAN
LLANDOVERY
TELYCHIAN
AERONIAN
rigidus
riccartonensis
murchisoni
centrifugus
crenulata
griestoniensis
crispus
turriculatus
SKIEN
PORSGRUNN
HOLMESTRAND
BÆRUM
MALMØYA
RINGERIKE
HADELAND
TOTEN
RINGSAKER
(gap)
Dark shales/ thin clastic turbidites
Thickly bedded clastics
Purple shales
Nodular limestones/ thinly bedded
Bioclastic limestones
Bioherms
G Graptolites
5 Eoplectodonta
4 Stricklandia/mid-shelf
3 Pentamerus (3⁺) no Pent.
2 Eocoelia (2) no Eocoelia.
1 Lingula/molluscs
+ incl. Palaeocyclus Erinostrophia

Fig. 6 The lithologies of the rocks shown in Fig. 4, together with the animal communities present.

the Vik Formation on Malmøya, and at the top of the Rytteråker Formation and at the base of the Vik Formation at Sandvika (Baarli 1990).

LATE LLANDOVERY AND EARLY WENLOCK FORMATIONS OF THE OSLO REGION

Vik Formation

This formation has its type area in the Ringerike district, where it has been divided into the Storøysundet, Garntangen and Abborvika Members (Worsley *et al.* 1983, p. 22) and where it is 80 m thick, as opposed to 55–70 m in the Oslo–Asker area. It overlies the Rytteråker Formation, which consists chiefly of bioclastic limestones (Möller 1987,1989). Although there are no continuous sections through the Vik Formation in the south of the Oslo Region, we estimate that the true thickness in the Skien and Porsgrunn districts is approximately 60–70 m. There is great lithological variation in the formation. Concretionary limestones with nodules at various sizes dominate the unit in Skien, Porsgrunn and Oslo-Asker, characteristically with smaller 'chicken-wire' nodules. Clastic content increases further north, and the three members in the type area are shale-dominated. The Storøysundet and Abborvika members are pale to dark reddish-brown shales, separated by the Garntangen Member's greenish-gray shales and nodular limestones. At Holmestrand (on Killingholmen Grid Ref. NL 752995) there is only a partial section which seems to represent the middle of the Vik Formation and consists of 5.5 m of shaley limestone followed by 1.5 m of more nodular limestone (but basically packstone or grainstone) and 16 m of thinly-bedded bioclastic limestone with shaley interlaminae, above which is the sea. Below this section there is an unexposed interval which we estimate at 12 m thickness of rock, underneath which Kiaer (1908, p.206) saw 2 m of shaley limestone which he also attributed to what we would now call the Vik Formation above the Rytteråker Limestone.

The dating of the Vik Formation has been achieved solely by evolving brachiopod lineages and to a lesser degree by palynomorphs — no graptolites have yet been found in the formation, and the species of *Stricklandia*, *Costistricklandia*, *Pentamerus* and *Pentameroides* have been noted above. In general, the distribution of the various animal communities (Fig. 6) shows a deepening upwards sequence from *Pentamerus* through *Stricklandia* to *Eoplectodonta* dominated assemblages. However, in the south of the area, in Skien, Porsgrunn and Holmestrand, there is a suggestion of an initial shallowing phase from *Stricklandia* to *Pentameroides* assemblages, although the sequence is much thinner there than to the north, for example in Ringerike. The succession in the Oslo district, for example in Malmøykalven, although not abundant in depth-diagnostic brachiopods, suggests oscillation amongst the dominant limestone facies, with notable variation from low- to high-energy sediments. Baarli (1990)

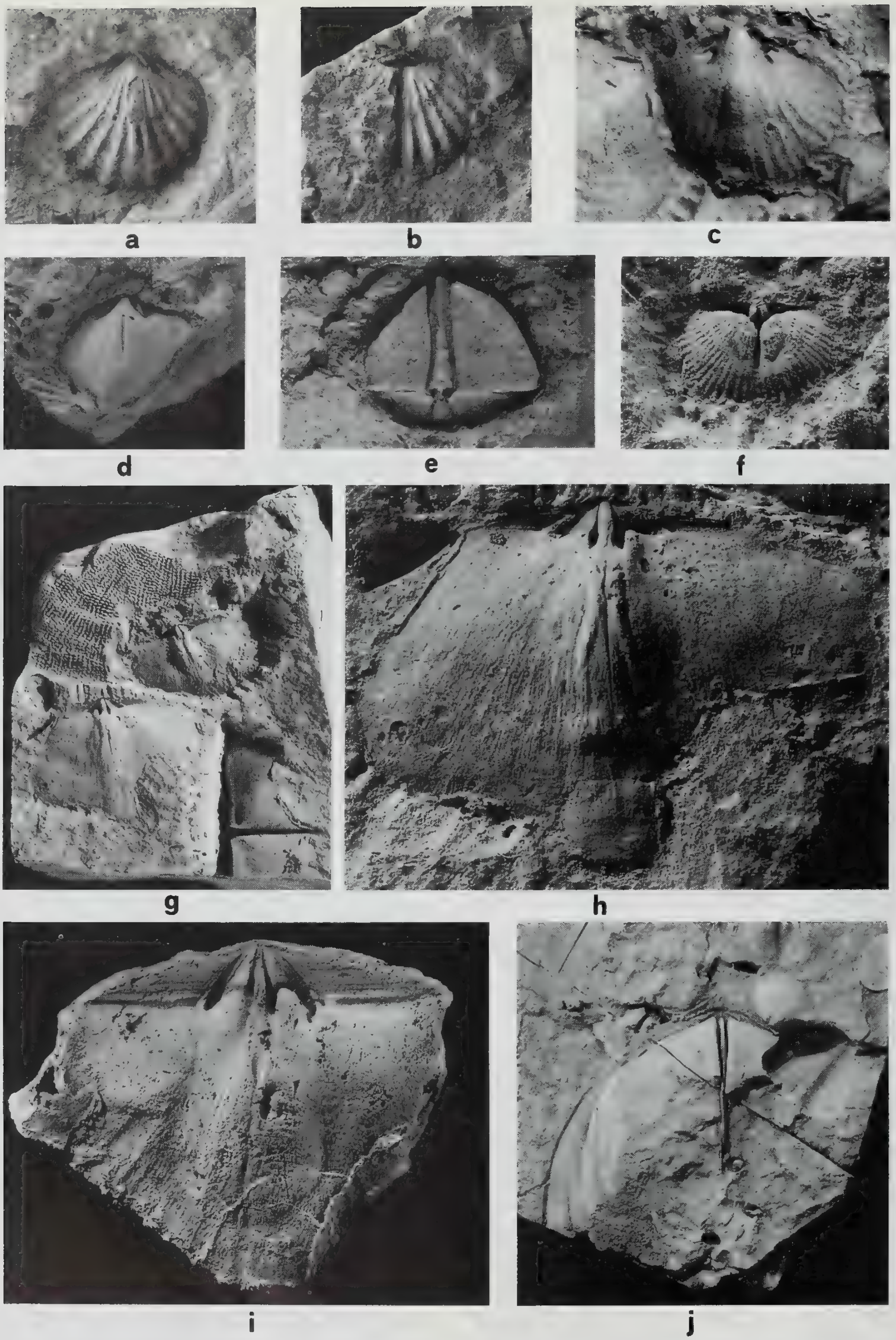

Fig. 7 Late Llandovery brachiopods from the Oslo Region. 7a–c, *Eocoelia hemisphaerica* (J de C Sowerby, 1839), internal moulds of two pedicle valves (BC 6509a, BC 6503), and a brachial valve (BC 6509b) from Rytteråker Formation, Hoppestad, Locality 11, 7a,b x 2.5; 7c x 4; 7d, *Eocoelia sulcata* (Prouty, 1923), internal mould of pedicle valve BC 6730 from Porsgrunn Formation, Holmestrand, Locality 3, x 2; 7e, *Cyrtia exporrecta* (Wahlenberg, 1818), internal mould of conjoined valves, BC 10584 from Porsgrunn Formation, Porsgrunn, Locality 22, x 2; 7f, *Skenidioides lewisii* (Davidson, 1848), internal mould of a brachial valve, BC 6290, from Vik Formation, Porsgrunn, Locality 17, x 4; 7g–1, *Stricklandia laevis* (J de C Sowerby, 1839), 7g, block BC 10716 showing internal moulds of two brachial valves and one pedicle valve, x 1; 7h, enlargement x 3 of the brachial valve in the lower left of Fig. 7g, from Vik Formation, Skien, Locality 25; 7i, internal mould of brachial valve BC 10505 from Vik Formation, Ringerike, Locality 34, x 3; 7j, *Pentameroides subrectus* (Hall & Clarke, 1893), internal mould of brachial valve, BC 6915, from Vik Formation, Porsgrunn, Locality 17, x 1.

has recorded a *Stricklandia* assemblage 18 m above the base of the Vik Formation at Malmøya above deeper water *Clorinda* assemblages in the lower 10 m, and below a probably deeper assemblage at 32 m. She also noted various ecological and sedimentological features in that section which indicate soft or even soupy substrates.

Ek Formation

The Ek Formation is confined to the north of the Oslo Region and is exposed in the Toten, Hamar and Ringsaker districts, where it consists of graptolitic shales without shelly fossils. There are no continuous sections, but the formation appears to be less than 100 m thick in Toten, Hamar and Ringsaker; Kiaer (1908) estimated approximately 95 m. In the Hadeland area, beds are present which are intermediate in lithological characters between the Ek and the Vik formations, for example in a railway cutting (Grid Ref. NM 787822 to 787825) and nearby series of temporarily exposed road-cuts near Jevnaker (e.g. at NM 781828) we have measured 98 m below the Bruflat Formation consisting of alternating reddish and grey-green shales and mudstones with occasional horizons with small nodules some of which include deeper-water shelly fossils such as *Clorinda, Eoplectodonta* and *Dicoelosia*. Below this section there is a gap representing an estimated 45 m of rock overlying 15 m of exposed Rytteråker Formation.

The dating of the Ek Formation has been achieved entirely by graptolites. Howe (1982, p. 23) has recorded the *turriculatus, crispus, griestoniensis* and *crenulata* zones from the formation. Apart from the deep water indicated both by the sediments and also by the absence of shelly faunas in Toten and Brummundal, there are no clear indications of depth fluctuations in the north of the region; however, in Hadeland some relative shallowing near the top of the sequence is indicated by the incursion of *Clorinda, Eoplectodonta* and *Dicoelosia* mentioned above.

Bruflat Formation

Although the original type section of this formation is near Bruflat in the Toten district (Strand & Størmer 1955, Skjeseth 1963), the section along the railway line near there (Grid Ref. NN 876238) shows only approximately 22 m of the formation, with neither a top nor a base visible and much faulting present. The best sections are in the Ringerike area, where D. Alm (pers. comm. 1985) has measured 120 m thickness; in the Hadeland area, where we have measured 182 m in a railway cutting 3 km north of Jevnaker (Grid Ref. NM 787822 to 787825) and in the Reinsvoll railway cutting, Toten (NN 881269), where we have measured 111 m of a section which we estimate to be 190 m thick in total. Although this is still one of the thickest formations present in the Silurian of the Oslo Region, our current measurements and estimates are much thinner than those previously published (e.g. the 400–500 m of Worsley *et al.* 1983, p. 27). The lithologies consist of greyish-green silty shales with individual units up to 1 m thick interbedded with thin to thick calcareous siltstones and sandstones in a coarsening-upwards sequence, with shell-lags of bioclastic limestones rich in shelly fossils near the top. In a single apparently unfossiliferous section near Reinsvoll, Toten (Grid Ref. NN 876270), we have measured 10 m of reddened beds in a faulted section which may be assigned to the Reinsvoll Formation (Worsley *et al.* 1983, p. 30), but the biostratigraphical significance of that formation is obscure.

The age of the Bruflat Formation is known from the *Costistricklandia lirata* found 30 m below the top of the formation in Ringerike and from the microfossils noted earlier. Dating in the Hadeland and Toten areas depends on the lower *crenulata* Zone graptolites in the underlying Ek Formation and in the *Erinostrophia–Palaeocyclus* assemblages found near the top of the formation (Fig. 8b–e) which indicate that the whole formation there, thick though it is, was laid down within *crenulata* Zone time. The Bruflat is a shallowing upward sequence, from the deeper-water Ek shales at its base to the near-shore molluscan dominated assemblages at the top of the formation.

Skinnerbukta Formation

This formation, which is 80 m thick in its type area at Skinnerbukta (Grid Ref. NM 894381) on Malmøya in the east of the Oslo district, overlies the Vik Formation in the Oslo and Asker districts. Apart from at Skinnerbukta itself, the Skinnerbukta Formation is poorly exposed and hence poorly documented, but we were fortunate in that there was a temporary exposure in 1986 through almost all of the formation near Øverland, Baerum (Grid Ref. NM 871444), where we were able to measure 91 m of shales and mudstones up to a 1 m transitional junction with the base of the overlying Malmøya Formation. Worsley *et al.* (1983, p. 30–31) also assigned Kiaer's 8a and 8b subdivisions to the Skinnerbukta Formation in the Skien, Porsgrunn and Holmestrand areas, but we now assign these beds to the new Porsgrunn Formation.

The age of the Skinnerbukta Formation is known from the graptolites recovered by Howe (1982) at Skinnerbukta itself and from the new finds reported above from the Baerum area, which together represent the *centrifugus, murchisoni* and *riccartonensis* zones of the early Sheinwoodian. There is an almost complete lack of shells near the base of the formation, but rather more shelly faunas occur progressively higher up; since the Skinnerbukta consists largely of turbidites, lateral displacement of these shells may have been considerable and so although a shallowing-upwards sequence is suggested, this cannot be proved. Thus the newly revised Skinnerbukta Formation can be considered to be entirely of Wenlock age (Fig. 5), and not reaching down into the Llandovery in places, as previously thought (Worsley *et al.* 1983).

Porsgrunn Formation

Above the Vik Formation and below the early Wenlock reefs of the Braksya Formation there are a variety of rocks, which are well exposed in the north of the Oslo Region (the Bruflat Formation of Toten, Hadeland and Ringerike) but poorly exposed from the Oslo–Asker districts southwards. These latter rocks have been grouped hitherto within the Skinnerbukta Formation (Worsley *et al.* 1983, p. 30), but in the present study it has become apparent that they are better divided into two separate formations: (a) the true Skinnerbukta Formation of Malmøya and Baerum, which are thin-bedded dark shales and calcareous turbidites now known to be of Wenlock age; (b) a new Porsgrunn Formation, which consists of a variety of deeper shelf, largely bioturbated chiefly mudstones, but with subsidiary siltstones and occa-

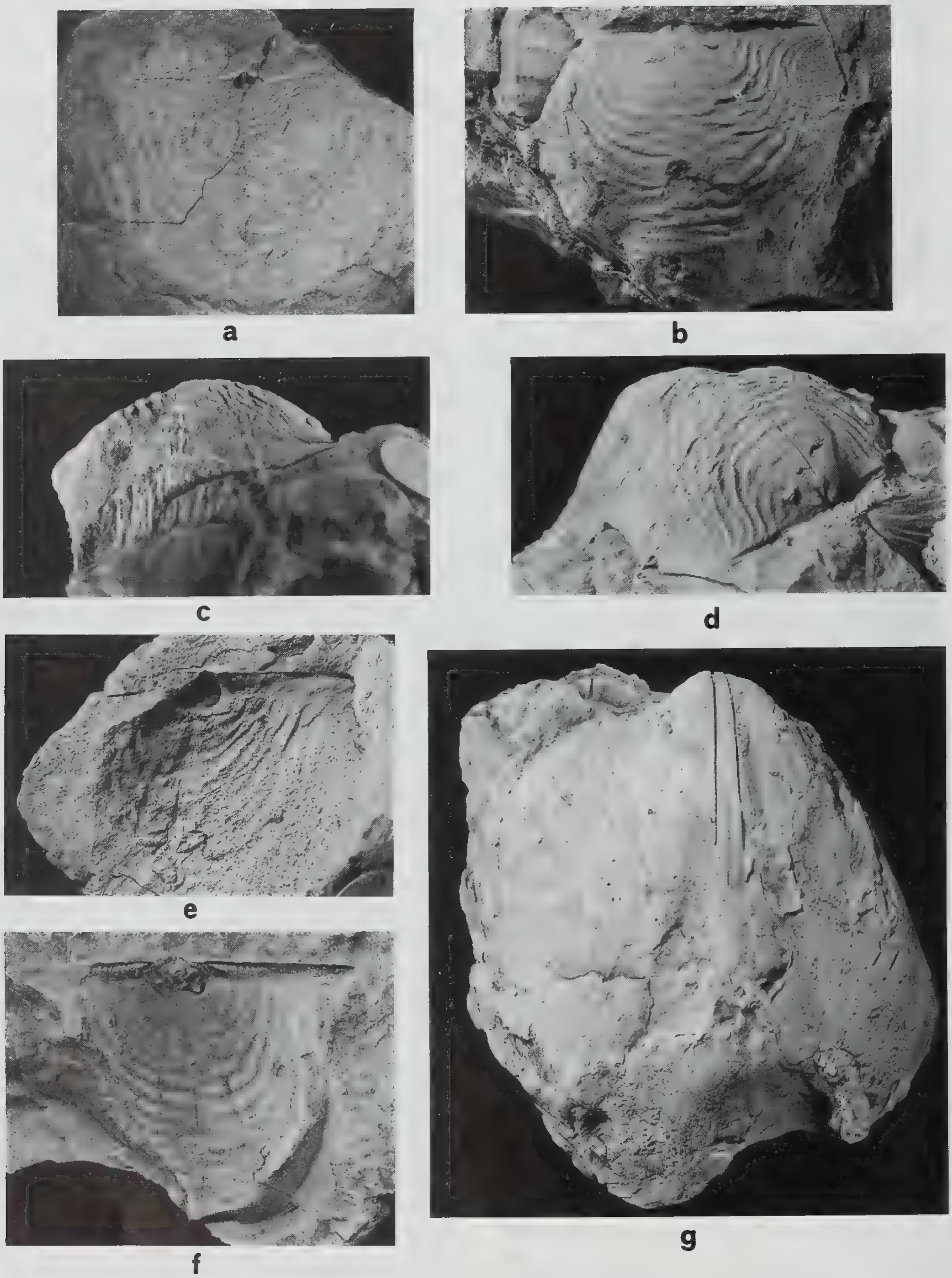

Fig. 8 Late Llandovery brachiopods from Ireland and the Oslo Region. 8a–f, *Erinostrophia undata* (M'Coy, 1846); 8a, internal mould of brachial valve, NMING F77475, lectotype selected Cocks (1978, p. 128), from Kilbride Sandstone, Egool, Ballaghadareen, Co. Mayo, Ireland, x 1; 8b–d, internal mould of a pedicle valve, BC 6686 from Bruflat Formation, Hadeland, Locality 14, x 1.5; 8e, internal mould of a brachial valve BC 6690 from the same locality, x 1.5; 8f, internal mould of a brachial valve from Porsgrunn Formation, Skien, Locality 4, x 1.5; 8g, *Pentamerus oblongus* J de C Sowerby, 1839, internal mould of a brachial valve, BC 10473 from Rytteråker Formation, Malmøykalven, Locality 28, x 1.5.

sional nodular limestones, which are all of late Llandovery age. The stratotype of the new formation is a series of discontinuous exposures along Øyekastveien, Porsgrunn (from Grid Ref. NL 369554 to 370555). The base is defined at NL 369554, where a 1.5 m transitional muddy limestone is seen from the underlying Vik Formation followed by massive mudstones with occasional shelly bands (e.g. Collection 22 at 5 m above the base). These are followed by siltstones and mudstones with thin carbonate horizons, much bioturbated, followed by a greater proportion of mudstones with (near the top) some thicker siltstones and larger limestone nodules developed, in which are seen numerous *Palaeocyclus* (Fig.4). The junction with the overlying Braksya Formation is clearly exposed, and the total thickness of the Porsgrunn Formation at its type section is estimated at 52 m.

Dating of the Porsgrunn Formation has also been achieved by the new finds of *crenulata* Zone graptolites together with *Eocoelia sulcata* in the Holmestrand district and by the association of *Erinostrophia* (Fig. 8f) and *Palaeocyclus* in the upper part of the formation in the Skien and Porsgrunn districts, indicating that the whole formation probably lies within the *crenulata* Zone. The faunal assemblages indicate a general shallowing upwards from the deeper-water *Eoplectodonta* bearing beds near the base to the *Palaeocyclus–Erinostrophia* horizons near the top of the formation.

Braksøya Formation

This formation was recognized by Worsley et al (1983) only in the Skien and Ringerike districts, but we have also found it overlying the Porsgrunn Formation at Kommersøya in the Holmestrand district. The formation consists chiefly of carbonate rocks and contains many bioherms. The age is determined by the occurrence of *Eocoelia sulcata* at Skien, and *E. angelini* in beds immediately overlying the formation in the type section at Braksøya, Ringerike. A faunal revision of the Braksøya has not been undertaken in the present work, although a sample tested for conodonts by H.A. Nakrem from Locality 7 proved barren.

DISCUSSION

This contribution augments and synthesises the rapidly growing body of biostratigraphical and sedimentological information which has been generated since Worsley et. al. (1983) established the present stratigraphical framework for the marine Silurian succession of the Oslo Region. The relationships depicted in Figs 5 and 6 are derived from a considerable database and the correlations are arguably as well constrained as present exposures will permit. It is therefore relevant to discuss the implications of these correlations and palaeobathymetric assignments for our understanding of the Oslo Region's development during the late Llandovery, especially taking into account recent developments elsewhere in the field of sequence stratigraphy and their applications to the genetic interpretation of rock sequences (e.g. Galloway 1989). The Oslo Region is particularly interesting in this respect as we may attempt to distinguish there between the effects of large-scale sea-level change and local tectonic imprint upon sequence development. We are naturally limited by the two-dimensional nature of Silurian exposures throughout the region, a feature not appreciably improved by attempts at palinspastic reconstruction (Fig. 9), but we can clearly distinguish the changing groupings of different districts with time.

In general terms we can recognise one depositional megasequence which is generally coincident with the Telychian, conforming to a full cycle between two major highstands in sea-level. These highstands have been suggested by Johnson et. al. (1991) to have large-scale — possible intercontinental — distributions. The base of this megasequence essentially coincides with the junction between the underlying Rytteråker and the overlying Vik or Ek formations in central and northern districts of the region. This transition represents a rapid deepening from shallow water carbonate shoals and patch reefs to the moderately deep shelf red shales and nodular limestones of the Vik Formation in Ringerike, Baerum and Oslo or to the deep shelf to basinal graptolitic shale environments of the Ek Formation in Hadeland and further north. As tentatively suggested by Bjørlykke (1983) and elaborated by Baarli (1990) this deepening may have been related to the development of a local basin as an isostatic response to nappe emplacement in the developing Caledonides to the northwest.

On present evidence the base of the Vik Formation may be penecontemporaneous both in the Ringerike and Oslo districts; there is insufficient evidence to either support or disprove the models of Møller (1988) and Baarli (1990) which suggest significant younging southeastwards from Ringerike to Oslo. However, the base of the formation in Skien does appear to be significantly younger than in either of these districts. Although the *Pentamerus*/*Pentameroides* transition is still not precisely dated, representatives of this lineage indicate that the basal Vik Formation in Skien correlates with the deepening trend suggested by the upper parts of the middle Garntangen Member of the formation in Ringerike.

The Vik Formation in Oslo and Baerum has earlier been suggested as representing ongoing deepening through the Telychian (Johnson & Worsley 1982). Increased knowledge of conodont faunas and benthic assemblages (Nakrem 1988, Baarli 1990) refute this suggestion, and indicate somewhat oscillating conditions, with a phase of more pronounced shallowing in the *crispus* to mid- *griestoniensis* biozones. Thus, throughout the Telychian these areas lay on the northern margins of a moderate depth nodular carbonate platform immediately south of a ramp development which sloped down into the Ek shale basin. The Ringerike district occupied an intermediate position between these regimes, with shale development at times of relevant highstand and carbonates around the *crispus* to *griestoniensis* phase with shallower conditions. As yet insufficiently studied or understood are the occurrences of intraformational conglomerates and possible slump/slide phenomena in the Vik Formation of Malmøya in the Oslo district itself, which perhaps indicate tectonic instability along the northern margins of the carbonate platform.

The development of the Bruflat Formation in the latest Llandovery offers more direct and compelling evidence of tectonic controls on the evolution of the area — not least when we examine the abrupt break in lithofacies and depositional styles between the Vik and Bruflat formations in the Ringerike district. Although the Bruflat Formation in its type area is thinner than was suggested by Worsley et al. (1983), this unit still represents depositional rates an order of magnitude larger than those shown by older sequences in the Oslo Region. As a direct corollary to the earlier development of a

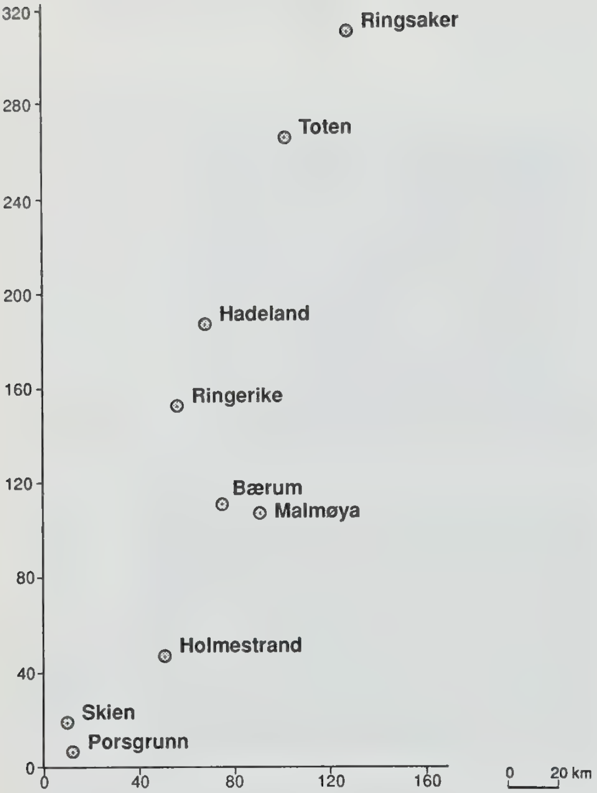

Fig. 9 Diagram showing the original relative positions of the various districts in the Oslo Region assuming a subsequent tectonic shortening of one third.

downwarped basin in the northern parts of the region, the development of the Porsgrunn Formation in southern districts suggests a deepening trend penecontemporaneous with the coarsening and shallowing-upwards sequence of the Bruflat Formation to the north. This southern deepening trend carried on through the *griestoniensis* and *crenulata* biozones before stabilisation in the latest Telychian.

Thus the picture which emerges suggests that the early Telychian highstand of the Oslo Region more probably reflected local tectonics than larger scale phenomena. Variations within the Telychian sequence itself also suggest local tectonic control, with profound variations in the northern districts and more subtle but still well-defined changes in the south. The entire depositional sequence terminated with general shallowing-upwards trends throughout the region. Both in Ringerike and in the southern districts there was an apparent depositional break before the development of the shallow-water carbonates of the Braksøya Formation; in sequence stratigraphy terms this break corresponds to a lowstand prior to the earliest Wenlock development of a maximum flooding surface marked by the clasts at the base of the formation. It is unfortunate that we have no direct evidence of the post-Telychian development in northern districts, although the red beds of the Reinsvoll Formation might represent back-lagoon lateral equivalents of the Braksøya Formation. The Telychian facies and subsidence patterns in the region were now reversed, as the sequence boundary in Oslo and Baerum suggests initially higher subsidence rates and development of a rimmed basin filled by the graptolitic shales of the Skinnerbukta Formation, prior to shoaling into the open marine carbonates of the Malmøya Formation. Thus, although the Telychian Stage may be a good operating unit in global terms because of its definition at base and top by sequence boundaries reflecting sea-level change; variation within the time interval suggests local isostatic response to nappe emplacement north-west of the present Oslo Region. The most marked variations are those nearest to the Caledonian Front in the northern districts, with more distal response first in Skien, and then in the earliest Wenlock in the Oslo district itself.

It would be relevant to continue this study into the Wenlock so that closer restraints could be imposed upon our knowledge of the final phase of marine sedimentation in the Oslo Region. However, there are greater problems in biostratigraphic precision in the Wenlock sequences. The platform carbonate deposits which dominate that succession contain benthic faunas which, although very useful for palaeoecological analyses, lack the coeval evolutionary lineages found in the shelly faunas of the Llandovery.

ACKNOWLEDGEMENTS.

We are most grateful to Dr R.B. Rickards and Dr N.J. Morris for identifying our graptolites and molluscs respectively. We also thank D. Alm for permission to use his measured section of the Ringerike district and acknowledge critical comments by G. Baarli, M.G. Bassett and M.E. Johnson on an earlier version of the typescript.

APPENDIX 1: A NEW GENUS OF BRACHIOPOD

Order **STROPHOMENIDA** King 1846

Superfamily **STROPHOMENACEA** King, 1846

Family **STROPHEODONTIDAE** Caster, 1939

ERINOSTROPHIA gen. nov.

TYPE SPECIES. *Orthis undata* M'Coy, 1846.

DIAGNOSIS. Like *Protomegastrophia* Caster, 1939, but with pronounced but discontinuous rugae over the whole shell and rounded rather than blade-like cardinal process lobes. Transverse socket ridges. No dental plates.

DISCUSSION. Only one species of this distinctive genus is so far known. A review of the genera close to the *Brachyprion–Megastrophia* plexus was undertaken by Harper & Boucot (1978), but the striking rugae of the new genus remain distinctive from all its relatives. The erect form of the cardinal process lobes of *Erinostrophia* and *Protomegastrophia* differs from the anterior-facing cardinal process lobes of *Brachyprion leda*, the type species of *Brachyprion*. A current review of stropheodontid brachiopods for the revised *Treatise on Invertebrate Paleontology* suggests that the form and position of the cardinal process lobes are the most important criteria for familial classification in this group. In the type species of *Erinostrophia* the denticles are present for approximately half the width of the hinge line. The absence of dental plates separates the new genus from the closely related *Eomegastrophia* which occurs in the later Aeronian Pentamerus Beds of Shropshire.

Erinostrophia undata (M'Coy, 1846) (Figs. 8a–f)

1846 *Orthis undata* McCoy, p.36, pl.3, fig.21
non 1852 *Leptaena undata* (M'Coy); M'Coy in Sedgwick & M'Coy, p.234, pl.1H, figs 38,39
1861 *Strophomena walmstedti* Lindström, p.372, pl.372, pl.13, fig.16
1868 *Strophomena walmstedti* Lindström; Davidson p.18, pl.13, fig.16
1871 *Strophomena walmstedti* Lindström; Davidson, p.290, pl.40, figs 6–8
non 1871 *Strophomena deltoidea* Conrad var. *undata* (M'Coy); Davidson, p.295, pl.39, figs 23.24
1974 *Megastrophia (Protomegastrophia) walmstedti* (Lindström); Bassett & Cocks, p.16, pl.3, figs 5–9
1978 *Megastrophia (Protomegastrophia) undata* (M'Coy); Cocks p.128
1978 *Brachyprion (Brachyprion) walmstedti* (Lindström); Harper & Boucot, p.16

TYPE SPECIMENS. Lectotype of *undata* (selected Cocks 1978, p.128) National Museum of Ireland, Dublin NMING: F7475 (previously registered NMI.G.20.1976), a brachial valve, the original of M'Coy 1846 pl. 3, fig 21 from Kilbride Sandstone (Telychian), Egool, Ballaghadareen, County Mayo, Ireland refigured here (Fig. 8A). Lectotype of *walmstedti* (selected Bassett & Cocks 1974, p.16) Naturhistoriska Riksmuseet, Stockholm, Sweden RMS Br 102367, conjoined valves, the original of Lindström 1861, pl.13, fig.16, from Lower Visby Beds (Telychian), Visby, Gotland, Sweden.

DISCUSSION. This species has been described and figured from Ireland, Gotland and the Pentland Hills, Scotland (Bassett & Cocks 1974, pl.3, fig 6) and has been well-known since the mid-nineteenth century. It was listed as *Strophomena walmstedti* by Kiaer (1908) from the Oslo Region, but not described or figured by him. *Erinostrophia undata* is common in the upper part of the Bruflat and Porsgrunn formations and appears to be restricted to rocks of later Telychian age (see above), both in Norway and elsewhere in Europe.

APPENDIX 2: LIST OF LOCALITIES

1. Porsgrunn Formation, shore exposure, Kommersøya, Holmestrand, NL 750989
2. Porsgrunn Formation, shore exposure, Kommersøya, 1.5m above Locality 1
3. Porsgrunn Formation, shore exposure, Kommersøya, 1.2m above Locality 2
4. Porsgrunn Formation, roadside 100m W of Gjerpen Church, Skien, NL 347654
5. Vik Formation, outcrop behind house, Hans Hauensgate, Skien, NL 351638
6. Porsgrunn Formation, old quarry by sports field, Kapitelberget, Skien NL 357629
7. Braksøya Formation, cliff at Kapitelberget, Skien, NL 357628
8. Porsgrunn Formation, side of football pitch, Skien, NL 361621
9. Porsgrunn Formation, football pitch, Skien, 20m above Locality 8
10. Porsgrunn Formation, garden outcrop, Skien, NL 372599
11. Rytteråker Formation, roadside near Tufte Farm, Skien, NL 336687
12. Saelabonn Formation, cliffs by road south of Skien, NL 369595
13. Bruflat Formation, railway cutting south of Reinsvoll, Toten, NN 881269
14. Bruflat Formation, roadside 300m N of Sogn, Hadeland, NM 785867
15. Vik Formation, shore exposure, Killingholmen, Holmestrand, NL 752995
16. Bruflat Formation, railway cutting 3km N of Jevnaker, Hadeland, NM 787825
17. Vik Formation, factory yard, Porsgrunn, NL 364553
18. Porsgrunn Formation, cliff at Kapitelberget, Skien, NL 357629
19. Vik Formation, road by sports ground, Kapitelberget, Skien, NL 367554
20. Porsgrunn Formation, outcrop by sports ground, Porsgrunn, NL 368554
21. Vik Formation, roadside outcrop, Øyekastvegen, Porsgrunn, NL 367546
22. Porsgrunn Formation, roadside outcrop, Øyekastvegen, Porsgrunn, NL 369553
23. Vik Formation, old quarry near Kapitelberget, Skien, NL 350637
24. Vik Formation, old quarry near Kapitelberget, Skien, 1.5m below Locality 23
25. Vik Formation, roadside outcrop, Hesthagveien, Skien, NL 357625
26. Skinnerbukta Formation, temporary exposure in building site 10m N of Jongsåsveien, Baerum, NM 846405
27. Skinnerbukta Formation, temporary exposure by house in Seljefløyten, Baerum, NM 827426
28. Rytteråker Formation, shore at Malmøykalven, Oslo, NM 978379
29. Vik Formation, shore at Malmøykalven, Oslo, NM 980381
30. Malmøya Formation, roadside at Daeliveien, Baerum, NM 859428
31. Skinnerbukta Formation, temporary exposure in hillside SE of Edelgranveien, near Øverland, Baerum, NM 871444
32. Vik Formation, roadside outcrop, Christians Skredvigsvei, Baerum, NM 863428
33. Skinnerbukta Formation, temporary exposure near Øverland, 36m below Locality 31
34. Vik Formation, shore exposure, S side of Purkøya, Ringerike, NM 688568
35. Skinnerbukta Formation, roadside outcrop Asterudveien, Baerum, NM 869442
36. Porsgrunn Formation, cliff exposure near shore, Kommersøya, 23.5m above Locality 3
37. Vik Formation, roadside outcrop by school gate, Skien, NL 365615
38. Steinsfjorden Formation, roadside at Øyekastvegen, Porsgrunn, NL 370555
39. Bruflat Formation, roadside outcrop, Garntangen, Ringerike, NM 720609

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Catalogue of the type and figured specimens of fossil Asteroidea and Ophiuroidea in The Natural History Museum

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INTRODUCTION

This is a catalogue index of the type and figured fossil starfishes and brittle-stars in the collections of the Department of Palaeontology, The Natural History Museum, London, and is complete up to May 1990. Only primary types have been included (i.e. holotype, lectotype, syntype, neotype), whether figured or not. Paratypes have been included only if they have been figured.

Like the preceeding catalogue on the type and figured fossil Echinoidea (Lewis, D. N. 1986 *Catalogue of the Type and Figured Specimens of Fossil Echinoidea in the British Museum (Natural History)*, it is divided into three parts. In the first part, which is divided into Asteroidea and Ophiuroidea, the genera are arranged alphabetically, with all the information about each specimen included therein. The second part is a bibliography of the works referred to in each entry. The third part is an alphabetical index of species, each being paired with the genus in which it is placed in the first part of the catalogue. The index also contains generic synonyms to which species had been previously assigned; these are printed in italics. At the end of the catalogue there are figures of type specimens which were not figured either in their original descriptions, or in subsequent publications.

The generic assignment of each species in the main entry of this catalogue is the name in current use for storage of the specimens in the collections. Where a name has been changed from that in a description or figuring, the original name is cross-referenced to the current name, where details of the specimen will be found.

The registration number of most specimens is prefixed by 'E' which refers to the registers (or catalogues) of fossil echinoderms in the Department of Palaeontology; no other invertebrate phylum has this prefix letter. Some registration numbers have the prefix 'OR' which refers to an older series of registers (**O**ld **R**egister) in which specimens of *all* phyla were registered. From the Spring of 1990, computerised registration of specimens commenced and the prefix 'EE' is given to registration numbers. However, there are no 'EE' prefixes in this catalogue.

Unless replicas of specimens have actually been figured, all the entries in the catalogue refer to real specimens.

Locality details are recorded in the catalogue as they appear in the register entry, on specimen labels and in the references. No county or country names have been brought up-to-date, as such alterations can be misleading or even incorrect. Stratigraphic details are recorded as they appear in register entries, references, and on specimen labels, and where possible have been brought up-to-date with current stratigraphic usage.

Records which include references to monographs published over a number of years by several authors, include in the entry the range of dates of the monograph. This is followed by a single date and the pagination for the record (e.g. Sladen, W. P. & Spencer, W. K. (1891-1908) 1905: 77, pl. 21 figs 2, 2a). The exact authorship can be found in the bibliography. Similarly, records which include references to monographs published over a number of years by a single author, include in the entry the range of dates of the monograph. This is followed by a single date and the pagination for the record (e.g. Spencer, W. K. (1914-1940) 1922: pl.16 fig.1). Because these monographs are frequently referred to by unofficial titles (e.g. 'Sladen & Spencer's Monograph', 'Spencer's Palaeozoic Monograph') this is probably less confusing than giving the actual author and date (e.g. Spencer, W. K. 1905: 77, pl. 21 figs 2, 2a).

It is inevitable that over a number of years information about specimens, or even specimens themselves, may be lost, particularly if collections are moved from place to place for various reasons. Fossils may also suffer from less than adequate storage methods and undergo decay. A prime example of this is a specimen of *Coulonia colei* (Forbes), a syntype of *Astropecten crispatus* Forbes, number OR 57501, figured herein, which was destroyed by pyritic decomposition probably as long ago as the 1920s. Included with the specimen are notes of treatment given to it in 1919, indicating that deterioration had already commenced.

The catalogue was compiled firstly on index-cards, then entered into the Museum Data-base System (MDS) via an Olivetti M 290 micro-computer linked to an Olivetti M 380 multi-user computer. MDS was devised and developed by Museum staff, principally by Mr. David French, and allows an ordered entry of data, with repeatable fields, into a data-base package written in 'C' under the 'Unix' operating system. Subsequent manipulation of data, report generation, and editing, can be carried out easily using the MDS. Editing can also be effected by conversion of the data to WordPerfect word-processing. A version of MDS is available for use on IBM AT and compatible micro-computers using MS-DOS.

I wish to thank Mr. Adrian Rissoné of the Department of Palaeontology for his considerable and essential help in all matters relating to the computers, Mr. Phil Hurst and Mr. Phil Crabb of the photographic staff of the Museum for the photographs and to Dr.Andrew Smith for helpful criticism.

TYPE AND FIGURED FOSSIL ASTEROIDEA

A

Archastropecten cf huxleyi (Wright)
E 28383 See: **Pentasteria (Archastropecten) cf huxleyi (Wright)**

Archastropecten huxleyi (Wright)
OR 33848 See: **Pentasteria (Archastropecten) huxleyi (Wright)**

Archastropecten portlandicus Hess
E 13739, E 13740a See: **Pentasteria (Archastropecten) portlandicus (Hess)**

Archophiactis grayae Spencer
E 52489 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 361, 362, 363, 364, text fig. 234, pl. 24 fig. 2 as *Archophiactis grayae* Spencer.

E 52642 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 356, 361, 362, text fig. 233A, 364, pl. 24 fig. 5 as *Archophiactis grayae* Spencer.

E 52693a,b Holotype of *Archophiactis grayae* Spencer. **Type species** of *Archophiactis Spencer 1927 : 361*. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1927: 361, 362, 363, pl. 24 fig. 4 (E 52693a); 356, 361, 362, 364, text fig. 232A, pl. 24 fig. 3 (E52693b) as *Archophiactis grayae* Spencer.

Arisaigaster leintwardinensis (Spencer)
E 13153 Holotype of *Mesopalaeaster(?) leintwardinensis* Spencer. Silurian. Lower Ludlow Shales. Leintwardine, Hereford, England. Colld Morton, G. H. Purchd of Miss Morton July 1900. Type figd Spencer, W. K. (1914–1940) 1916: 89–90, text fig. 49; 1919: 179, pl. 2 fig. 5 as *Mesopalaeaster(?) leintwardinensis* Spencer.

Arthraster cristatus Spencer
E 13252 Cretaceous, Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 140, 177, pl. 16 fig. 7.

E 20266 Holotype. Cretaceous, Santonian, *coranguinum* Zone. Micheldever, Hampshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 93, pl. 29 figs 10, 10a,b.

Arthraster dixoni Forbes
E 5024 Cretaceous, Upper Santonian. *Marsupites* band. Cliffs, east of Brighton, Sussex, England. Presd McPherson, W. 3rd May 1902. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 91, pl. 29 figs 11, 11a.

OR 47000 Holotype. **Type species** of *Arthraster* Forbes 1848 : 467. Cretaceous, Cenomanian. Lower Chalk. Balcombe Pit, near Amberley, Sussex, England. Dixon, F. Colln 1850. Type refd Forbes, E. 1848: 467. Figd Forbes, E. *in* Dixon, F. 1850: 336, pl. 23 fig. 1. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 369, 370, 440, pl. 23 fig. 1. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: pl. 18 figs 1, 1a; 1907: 91–93.

'Asterias' gaveyi (Forbes)
E 1638 Holotype of *Uraster gaveyi* Forbes. Jurassic, Pliensbachian, *capricornus* Zone. Middle Lias. Mickleton Tunnel, near Chipping Campden, Gloucestershire, England. Colld Gavey, G. E. Wright, T. Colln. Purchd Butler, F. H. May 1887. Type figd Forbes, E. 1850b: 1–2, pl. 2 figs 1,2 as *Uraster gaveyi* Forbes. Figd Wright, T. (1863–1880) 1863: 100–101, pl.1 figs 1a,b as *Uraster gaveyi* Forbes.

Astropecten armatus Forbes
OR 57503 See: **Coulonia colei (Forbes)**

Astropecten cotteswoldiae Buckman
E 1633, E 1634, E 1635, E 1636 See: **Pentasteria (Archastropecten) cotteswoldiae (Buckman)**

Astropecten cotteswoldiae var. stamfordensis Wright
OR 75797 See: **Pentasteria (Archastropecten) cotteswoldiae (Buckman) var. stamfordensis (Wright)**

Astropecten cotteswoldiae var. stonesfieldenses Wright
E 2588 See: **Pentasteria (Archastropecten) cotteswoldiae (Buckman) var. stonesfieldensis (Wright)**

Astropecten crispatus Forbes
OR 57501 See: **Coulonia colei (Forbes)**

Astropecten granulatus Rasmussen
E 53626,28–29 Eocene, Bartonian. Middle Barton Beds, horizon E. Barton-on-Sea, Hampshire, England. Davis, A.G. Colln. Figd Rasmussen, H. W. 1972: pl. 3 figs 5a,b (E 53626), 7a,b (E 53628), 8a,b (E 53629). E 53629 was noted missing in May/June 1973 during curation and has not been found.

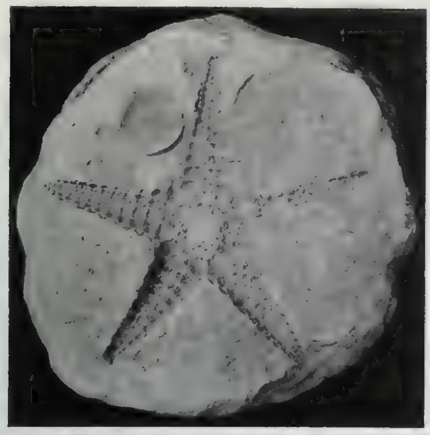
Fig. 1 *Siluraster caractaci* (Gregory), E 52857a,b, holotype, from the Ordovician, Caradoc, of Church Stretton, Shropshire: (a) aboral; (b) oral views of the specimen in the nodule. The specimen was photographed, lightly coated with ammonium chloride sublimate. Mag. x 1.8.

Fig. 2 *Stauranderaster gibbosus* Spencer, E 13239, holotype, from the Cretaceous *A. quadratus* zone, of Rottingdean, Sussex; two views of the specimen showing considerable disruption of the structure: (a) aboral view; (b) oral view. Mag. x 0.9.

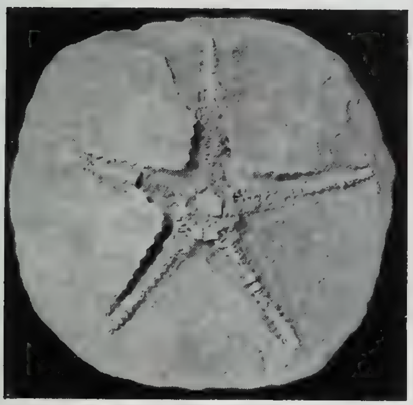
Fig. 3 *Coulonia colei* (Forbes), OR 57501, syntype of *Astropecten crispatus* Forbes, from the Eocene, London Clay, of the Isle of Sheppey, Kent. Compare its present condition with the original figuring by Forbes, 1849, pl. 3 fig. 3a. This is a prime example of what happens to some specimens when storage conditions are inadequate; even the labels were affected by the decomposition of the specimen, but fortunately not sufficient to erase all data. Mag. x 0.9.

Fig. 4 *Ophiura wetherelli* Forbes, E 2670, syntype, from the Eocene, London Clay, of the Isle of Sheppey, Kent. This was not the specimen figured by Forbes even though a label with the specimen says so. The first figuring of the specimen was by Busk, 1866, pl. 12 figs 4a–d, but although the figure is too small to be useful, it does show that the specimen was not the one figured by Forbes. Mag. x 2.7.

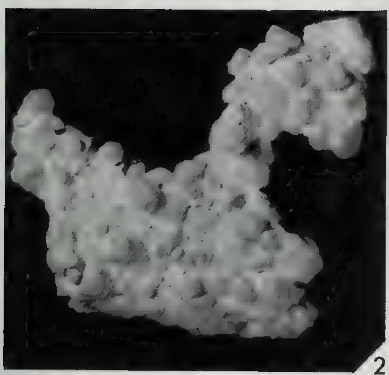
Fig. 5 *Ophiura wetherelli* Forbes, E 2650, ?syntype, from the Eocene, London Clay, of Highgate Archway, north London. This block contains many specimens throughout its structure and is one of three blocks from the same locality and from the Wetherell Collection. It is probably one of the specimens referred to by Forbes and if so, is a syntype. Mag. x 1.8.



1a



1b



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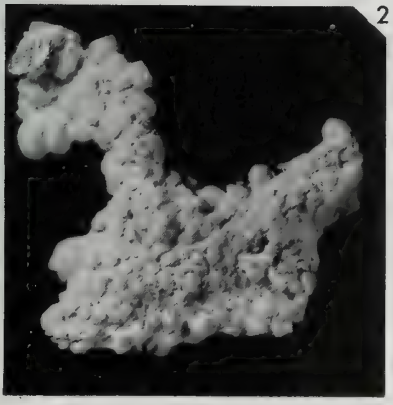

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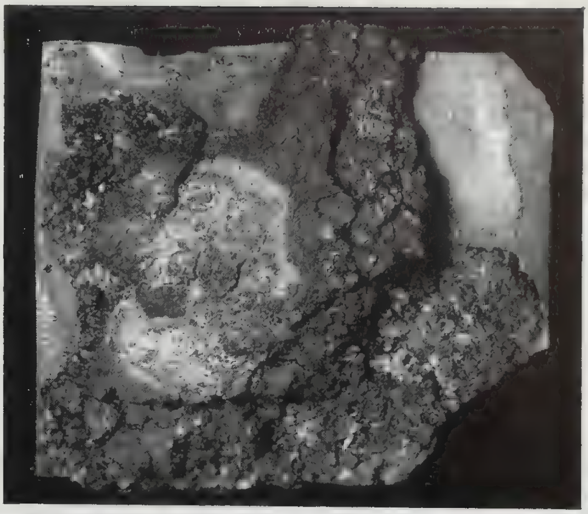

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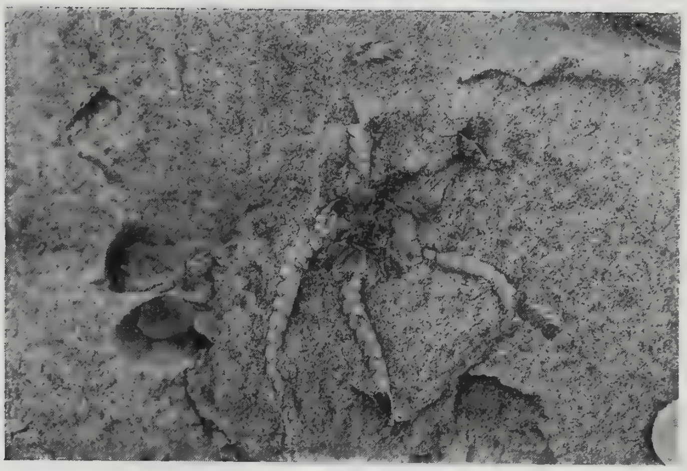

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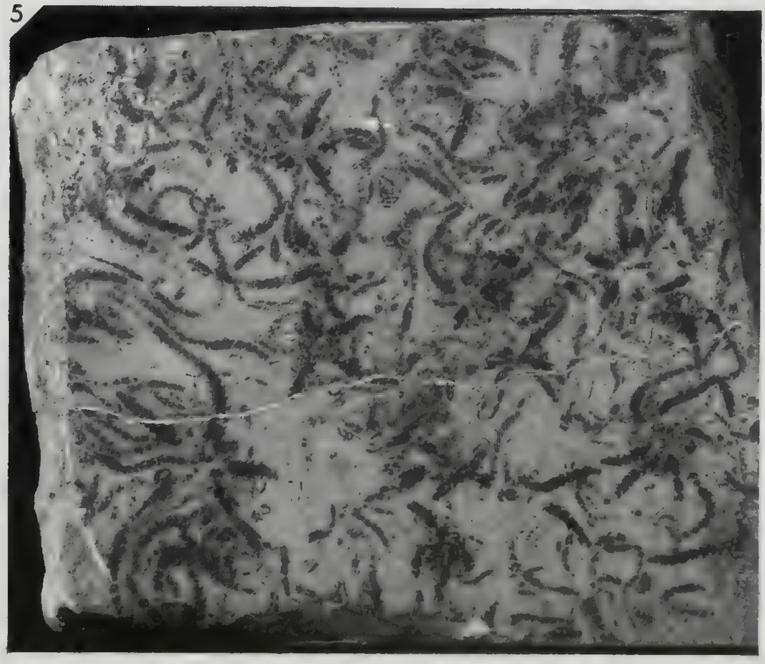

5

E 53627 Holotype. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton–on–Sea, Hampshire, England. Davis, A.G. Colln. Type figd Rasmussen, H. W. 1972: 38–40, pl. 3 figs 6a,b.

Astropecten huxleyi Wright
OR 33848 See: **Pentasteria (Archastropecten) huxleyi (Wright)**

Astropecten lorioli Wright
E 1639 See: **Pentasteria (Archastropecten) lorioli (de Loriol)**

'Astropecten' pichleri von Wöhrmann
E 53794 Triassic. Cassian, bed e4. Section VI, Veszprém, Bakony, Hungary. No collection data. Figd Bather, F. A. 1909: 235–236, pl. 13 figs. 435–437 as *Astropecten pichleri* von Wöhrmann.

'Astropecten' sp.
E 13573–4 Jurassic, Bathonian. Great Oolite. Bath, Somerset, England. Wright, T. Colln? Figd Wright, T. (1863–1880) 1863: pl. 8 fig. 3 (E 13573), 4 (E 13574) as ossicula of Asteriidae.
E 13575–7 Jurasssic, Bathonian. Great Oolite. Bath, Somerset. Wright, T. Colln? Figd Wright, T. (1863–1880) 1863: pl. 8 fig. 6 (E 13575), 7 (E 13576), 8 (E 13577) as *Astropecten* sp.

Astropecten wittsii Wright
E 1637 See: **Pentasteria (Archastropecten) wittsii (Wright)**

B

Baliactis devonicus Spencer
E 13628 Holotype. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd April 1910. Type figd Spencer, W. K. (1914–1940) 1927: 376, 378, 379, text figs 243, 244, pl.24 fig. 1 (all referred to as E 13625).

Baliactis ordovicus Spencer
E 52348 Holotype. Type species of *Baliactis* Spencer, 1927: 375–376. Upper Ordovician, Caradocian. Habberley Brook, Pontesford, Shropshire, England. Colld Audley, A. Shrewsbury Museum. Exch. November 1956. Figd Spencer, W. K. (1914–1940) 1922: pl. 17 fig. 1; 1927: 376, text fig. 242, 377–378. Type refd Owen, H. G. 1965: 560. Selected by Owen as the type by monotypy. See also his note on p. 560.

C

Caletaster sp
E 54083 Cretaceous, Cenomanian. Wilmington Sands, 6.58m below datum. The White Hart Sand Pit, Wilmington, Devon, England. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 202, 203, 207, pl. 42 figs 6a,b.

Calliderma hamptonensis (Wright)
E 1066 Holotype of *Goniaster hamptonensis* Wright. Jurassic, Bathonian. Great Oolite, 'planking beds' freestone. Minchinghampton Common, Gloucestershire, England. Colld Day, E., purchd from him by Buckman. Buckman, J. Colln. Type figd Wright, T. (1863–1880) 1863: 109–110, pl. 2 figs 2a,b as *Goniaster hamptonensis* Wright.

Calliderma latum Forbes
E 3347, E 3348, OR 35504, OR 47001 See: **Calliderma latum (Forbes)**

Calliderma latum (Forbes)
E 3347 Cretaceous. England. Capron, J. R. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 13, 14, pl. 2 figs 2a–d as *Calliderma latum* Forbes.
E 3348 (ex. 76002) Cretaceous, Cenomanian, *subglobosus* Zone. Sussex, England. Capron, J. R. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 13, 14, pl. 2 figs 1a–e as *Calliderma latum* Forbes.
OR 35504 Syntype of *Goniaster* (*Astrogonium*) *latus* Forbes. Cretaceous, Cenomanian, *subglobosus* Zone. Amberley, Sussex, England. Dixon, F. Colln. Type refd Forbes, E. 1848: 474 as *Goniaster* (*Astrogonium*) *latus* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 333, pl. 23 fig. 4 as *Goniaster* (*Astrogonium*) *latus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 367, 370, 440, pl. 23 fig. 4 as *Goniaster* (*Astrogonium*) *latus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 12–14, pl. 3 figs 1a–e as *Calliderma latum* Forbes.
OR 35505 See: **Calliderma smithiae (Forbes)**
OR 47001 Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Dover, Kent, England. Old Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 13, 14, pl. 3 figs 2a,b as *Calliderma latum* Forbes.

Calliderma mosaicum Forbes
E 2574, E 2602, E 2620, E 13049 See: **Calliderma smithiae (Forbes)**

'Calliderma smithiae' (Forbes)
E 3346 See: **Calliderma smithiae (Forbes)**

Calliderma smithiae Forbes
OR 48080, OR 75997, E 20973–74 See: **Calliderma smithiae (Forbes) Calliderma smithiae (Forbes)**
E 5063 See: **Ophryaster sulcatus (Sladen)**

Calliderma smithiae (Forbes)
E 2574 Cretaceous, Cenomanian. Lower Chalk. England. Old Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 10, 11, pl. 5 figs 2a–e as *Calliderma mosaicum* Forbes;1907: 123 as *Calliderma smithiae* (Forbes). Figd Gale, A. S. 1988 (1987a): 159, 170, 171, pl. 1 fig. 1.
E 2602 Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Dover, Kent, England. Smith, Mrs M. H. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: pl. 6 fig. 1 as *Calliderma mosaicum* Forbes;1907: 123 as *Calliderma smithiae* (Forbes).
E 2620 Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Dover, Kent, England. Smith, Mrs M. H. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 11, pl. 6 fig. 2a–c as *Calliderma mosaicum* Forbes; 1907: 123 as *Calliderma smithiae* (Forbes).
E 3346 (ex. 76002) Cretaceous, Cenomanian. Lower Chalk. Dorking, Surrey, England. No collection data. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 5, 10, pl. 7 figs 4a–c as *Calliderma mosaicum* Forbes; 1907: 123 as *'Calliderma smithiae' (Forbes)*.
E 13049 (ex. 76002) Cretaceous, Cenomanian. Lower Chalk. Cowslip Pit, county unknown, England. Purchd Capron, H. 1879. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: pl. 12 figs 4a–d as *Calliderma mosaicum* Forbes. No other information, either in the registers or with

the specimen, indicates the location of Cowslip Pit.

E 20969–70 Cretaceous, Campanian, *mucronata* Zone, 'L'. Norfolk, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 173, pl.12 figs 25 upper (E 20969), lower (E 20970).

E 20973–74 Cretaceous, Turonian, *cuvieri* Zone. Branscombe, Devon, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 127, 173, pl.12 figs 22 upper (E 20973), lower (E 20974) as *Calliderma smithiae* Forbes.

OR 35505 **Syntype** of *Calliderma latum* (Forbes). Cretaceous, Cenomanian, *subglobosus* Zone. Washington, Sussex, England. Dixon, F. Colln. Type refd Forbes, E. 1848: 474 as *Goniaster* (*Astrogonium*) *latus* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 333–334, pl. 23 fig.5 as *Goniaster* (*Astrogonium*) *latus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 367, 370, 440, pl. 23 fig. 5 as *Goniaster* (*Astrogonium*) *latus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 5, 13, pl. 3 figs 3a,b as *Calliderma latum* (Forbes). Figd Gale, A. S. 1988 (1987a): 161, 170, 171, pl. 2 fig. 2.

OR 48080 Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Dover, Kent, England. No collection data. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 5, 7, 9, pl. 8 figs 2a–e as *Calliderma smithiae* Forbes.

OR 75997 **Holotype** of *Goniaster* (*Astrogonium*) *smithii* Forbes. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Burham, Kent, England. Smith, Mrs M. H. Colln. Type refd Forbes, E. 1848: 474–475 as *Goniaster* (*Astrogonium*) *smithii* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 334, pl. 22 figs 1, 2 as *Goniaster* (*Astrogonium*) *smithii* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 367, 370, 439, pl. 22 figs 1, 2 as *Goniaster* (*Astrogonium*) *smithiae* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 5–9, pl. 1 figs 1a–f as *Calliderma smithiae* Forbes. Figd Gale, A. S. 1988 (1987a): 159, 170, 171, pl. 1 fig. 2 (referred to E 3349).

Chomataster acules Spencer

E 13255 **Holotype**. **Type species** of *Chomataster* Spencer 1913 : 128–129. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 128–129, 177, pl. 16 figs 8, 9.

E 13256–59 **Paratypes**. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 177, pl. 16 figs 10 (E 13256), 11, 11a (E 13257), 12 (E 13258), 13 (E 13259).

E 13260–61 **Paratypes**. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 128–129, 173, pl. 12 figs 28 upper (E 13260), lower (E 13261).

E 13262 **Paratype**. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 128–129, 173, pl. 12 fig. 3. Fig. 3 is an arm reconstructed from several ossicles.

Chomataster coombii (Forbes)

E 13724 See: **Nymphaster coombii (Forbes)**

Chomataster humilis Schulz & Weitschat

E 28407a,b See: **Nymphaster humilis (Schulz & Weitschat)**

Chomataster marginatus (Sladen)

OR 35484 See: **Nymphaster marginatus Sladen**

Chomataster praecusor Spencer

E 20971–72 Cretaceous, Campanian, *mucronata* Zone, 'M'. Studland, Dorset, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 129, 173, pl.12 figs 26 upper (E 20971), lower (E 20972).

Cnemidactis girvanensis (Schuchert)

E 52383 **Holotype** of *Urasterella girvanensis* Schuchert. **Type species** of *Cnemidactis* Spencer, 1918 : 156. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Nicholson, H. A. & Etheridge, R. 1880: 325–326, pl. 21 figs 9, 10 as *Tetraster* sp. Type figd Schuchert, C. 1915: 165, 175, 186, pl. 28 fig. 5 as *Urasterella girvanensis* Schuchert. Type refd Spencer, W. K. (1914–1940) 1918: 156 as *Cnemidactis*. The figuring by Schuchert is of a squeeze made from the actual specimen which is stored in the United States National Museum, numbered 60611.

E 52397a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 156, 159, text figs 102, 161, pl. 11 fig. 2 (E 52397b).

E 52444a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 156, 158, pl. 12 fig. 2 (E 52444a); 156, 157, text figs 101, 158, 161, 168, pl. 12 fig. 4 (E 52444b).

E 52453a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 156, 157, text figs 100, 158, (E 52453a).

E 52484a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 156, 161, pl. 12 fig. 5 (E 52484b).

E 52499 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 156, 157, pl. 13 fig. 2.

E 52589a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 156, 159, pl. 11 fig. 1 (E 52589a).

E 52590a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 156, 157, 158, 159, pl. 12 fig. 1 (E 52590a); 156, 158, pl. 12 fig. 3 (E 52590b).

E 52897a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Presd by Misses Gray June 1937. Figd Smith, A. B. *in* Murray, J. W. (editor) 1985: fig. 7.6.2 (E 52897a).

E 53835a–c Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Figd Gale, A. S. 1987b: 119 figs 7A,C (E 53835a).

Coccaster bulbiferus Spencer

E 13956 Holotype counterpart. **Type species** of *Coccaster* Spencer, 1916 : 75. Silurian. Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Ludlow Museum Colln. Purchased January 1947. Type figd Spencer, W. K. (1914–1940) 1916: 62, 66, 75–78, text figs 32I, 33, 39, 97; 1919: 179, text fig. 122a, pl. 3 fig. 2. The specimen is the counterpart of the part which is in the Royal Scottish Museum, Edinburgh, number 65/158a (as given by Spencer, pl. 2 fig. 1).

Compsaster petaliformis (Stürtz)

E 5003 Holotype of *Jaekelaster petaliformis* Stürtz. Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Type figd Stürtz, B. 1900 (1899): 235–236, pl. 4 figs 13–16 as *Jaekelaster petaliformis* Stürtz.

Compsaster spiniger (Wright)

E 1642 Holotype of *Uraster spiniger* Wright. Jurassic, Bathonian. Forest Marble. Near Road, Wiltshire, England. Colld Parsons, H. F., Wright, T. Colln. Purchd Butler, F. H. May 1887. Type figd Wright, T. (1863–1880) 1880: 166–168, text fig. 41 (fig. is reversed), pl. 21 fig. 1 as *Uraster spiniger* Wright. Figd Wright, T. 1886a: 50–52, text fig. on p. 51 as *Uraster spiniger* Wright. The text figure on p. 51 of Wright, 1886a, is reversed.

Comptonia comptoni Forbes

OR 34311 See: **Comptoniaster comptoni (Forbes)**

Comptonia elegans Gray

E 2567 Neotype. **Type species** of *Comptonia* Gray 1840 : 278. Cretaceous, Albian. Upper Greensand. Blackdown, Devon, England. Bowerbank Colln. Type refd Gray, J. E. 1840: 278. Figd Forbes, E. *in* Dixon, F. 1850: 336, pl. 22 fig. 9. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 369, 370, 439, pl. 22 fig. 9. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 71–72, pl. 17 figs 4, 4a. The justification for the selection of this specimen as the neotype is given by Spencer on p. 71.

Comptoniaster comptoni (Forbes)

E 54081 Cretaceous, Cenomanian. Wilmington Sands, 6.71m below datum. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 197, 202, pl. 41 figs 5a,b. **OR 34311 Syntype** of *Goniaster* (*Stellaster*) *comptoni* Forbes). Cretaceous. Upper Greensand. England. Bowerbank Colln. Type refd Forbes, E. 1848: 476 as *Goniaster* (*Stellaster*) *comptoni* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 69, 70, pl. 17 figs 3, 3a–b as *Comptonia comptoni* Forbes.

Coulonia colei (Forbes)

E 428a–g Eocene, Ypresian. London Clay, division 5. Highgate, North London, Middlesex, England. Presd Maitland, R. 1st October 1884. Figd Rasmussen, H. W. 1972: 43, pl. 3 fig. 9, pl. 12 fig. 1 (E 428a), pl. 3 figs 10a,b (E 428b), figs 11a,b (E 428c), figs 12 left (E 428d), right (E 428e), 13 left (E 428f), right (E 428g) (under E 428). E 428b–g are individual components of a single arm – E 428a – with suffixes for indentification.

OR 38490 Eocene. London Clay. Sheppey, Kent, England. Griffiths, W. Colln January 1858. Figd Rasmussen, H. W. 1972: 43, pl. 3 fig. 14 (under E 38490).

OR 57501 Syntype of *Astropecten crispatus* Forbes. Eocene. London Clay. Isle of Sheppey, Kent, England. Bowerbank Colln. Purchd 1865. Type refd Forbes, E. 1848: 479 as *Astropecten crispatus* Forbes. Figd Forbes E. 1849: 3, fig. 3 as *Astropecten crispatus* Forbes. The specimen has been totally destroyed by pyrite decomposition. According to a note included with the specimen, this occurred perhaps between 1931–1939, but probably started long before, as treatment with paraffin wax had been given in 1919. Figured herein, fig. 3.

OR 57503 Holotype of *Astropecten armatus* Forbes. Eocene. London Clay. Isle of Sheppey, Kent, England. Bowerbank Colln. Type refd Forbes, E. 1848: 479 as *Astropecten armatus* Forbes. Figd Forbes E. 1849: 3, fig. 4 as *Astropecten armatus* Forbes. Figd Forbes, E. 1852: 29, pl. 4 figs 1a,b as *Astropecten armatus* Forbes. Fig. 1a in Forbes 1852, is reversed left–right; it is a mirror image.

Coulonia sp

E 54168 Cretaceous, Lower Cenomanian. Loose, *or* 11.5m below datum, Bed A1. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 207, 208 pl. 43 fig. 4. The text (p.207) states that E 54168 was found loose, but the plate explanation indicates 11.5m below datum, from Bed A1. The explanation of pl. 43 gives the specimen as fig. 7, but there is no fig. 7 on pl. 43; the correct figure is that labelled 4, centre left on the plate.

Crateraster favosus (Spencer)

E 13238 Holotype of *Teichaster favosus* Spencer. Cretaceous, Upper Campanian, *mucronata* Zone. Studland, Dorset, England. Faber Colln. Exch Mineralogy Museum, University of Copenhagen 7th October 1912. Type figd Spencer, W. K. 1913: 122–123, pl. 12 fig. 14 as *Teichaster favosus* Spencer. Locality information given by Spencer on p. 173 is 'Isle of Wight'. Elsewhere – on p. 122, on labels and in the register – the locality given is Studland, Dorset.

E 13297–301 Paratypes of *Teichaster favosus* Spencer. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: E 13297–8: 122, 173, pl. 12 figs 16 (E 13297 = upper, E 13298 = lower); 177, pl. 16 figs 14 (E 13299), 15 (E 13300), 16a,b (E 13301) as *Teichaster favosus* Spencer.

E 20280 Cretaceous, Campanian, *mucronata* Zone. Clarendon, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Gale, A. S. 1988 (1987a): 181, 183, pl. 7 fig. 11.

Crateraster quinqueloba (Goldfuss)

E 2036 Cretaceous. Upper Chalk. Kent, England. Purchd Harford, F. June 1888. Figd Gale, A. S. 1988 (1987a): 172, 177, pl. 5 fig. 17.

E 2582 Paratype of *Pentagonaster megaloplax* Sladen. Cretaceous, Senonian. Upper Chalk. South–east England, England. Old Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 28, pl. 4 figs 3a–c as *Pentagonaster megaloplax* Sladen; 1907: 108 as *Pentagonaster quinqueloba* (Goldfuss).

E 5064 (ex. 46782) **Paratype** of *Pentagonaster megaloplax*

Sladen. Cretaceous, Senonian. Upper Chalk. Near Bromley, Kent, England. Simmons, J. Colln. Purchd 1869. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 28, 29, pl. 4 figs 4a–e as *Pentagonaster megaloplax* Sladen; 1907: 108 as *Pentagonaster quinqueloba* (Goldfuss).

E 5065 (ex. 35500) **Holotype** of *Pentagonaster megaloplax* Sladen. Cretaceous, Senonian. Upper Chalk. Sussex, England. Dixon, F. Colln. Figd Forbes, E. *in* Dixon, F. 1850: 333, pl. 23 fig. 9 as *Goniaster* (*Astrogonium*) *lunatus* Woodward. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 366, 370, 440, pl. 23 fig. 9 as *Goniaster* (*Astrogonium*) *lunatus* Woodward. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 27–29, pl. 4 figs 2a–c as *Pentagonaster megaloplax* Sladen; 1907: 108 as *Pentagonaster quinqueloba* (Goldfuss).

E 20279 Cretaceous, Santonian, *coranguinum* Zone. Micheldever, Hampshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Wright, C. W. & Smith, A. B. 1987: 216, pl. 47 fig. 4. Figd Gale, A. S. 1988 (1987a): 177, 179, pl. 6 fig. 7.

E 20968 Cretaceous, Campanian, *mucronata* Zone. Studland, Dorset, *or* Isle of Wight, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 121, 173, pl. 12 fig. 13. On a label with the specimen, E. R. Bush (once an Experimental Officer curator in the Department of Palaeontology) wrote ' . . . According to W. K. Spencer's small card label, the locality for this specimen is Studland, but in the Explanation of Plate 12 figures (. . . p.173) it is given as Isle of Wight.' The label is dated 6/12/51.

E 20975–76 Cretaceous, Turonian, *cuvieri* Zone. Branscombe, Devon, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 121, 173, pl. 12 figs 1 upper, 2 upper, 3 (E 20975); 1 lower, 2 lower, 4 (E 20976).

OR 46779 Cretaceous, Senonian. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. 10th May 1869. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 30, pl. 13 figs 1a,b as *Pentagonaster megaloplax* Sladen; 1907: 108 as *Pentagonaster quinqueloba* (Goldfuss).

D

Devonistella filiciformis (Woodward)

E 13638 **Syntype** of *Helianthaster filiciformis* Woodward. **Paralectotype.** Devonian. Great Inglebourne, Harberton, South Devon, England. Champernowne, A. Colln. Purchd July 1909. Type figd Woodward, H. 1874: 7–10, fig. on p. 8 as *Helianthaster filiciformis* Woodward. Figd Spencer, W. K. (1914–1940) 1927: 369, 370; 1930: pl. 25 fig. 3 (in error as E 13639a).

E 13639 **Syntype** of *Helianthaster filiciformis* Woodward. **Lectotype**. **Type species** of *Devonistella* Spencer, 1927 : 369. Devonian. Great Inglebourne, Harberton, South Devon, England. Champernowne, A. Colln. Purchd July 1909. Type refd Woodward, H. 1874: 7–10 as *Helianthaster filiciformis* Woodward. Figd Spencer, W. K. (1914–1940) 1927: 369, 370 text fig. 236; 1930: pl. 25 figs 1, 2 (in error numbered E 13639b).

E

Echinasterella sladeni Stürtz

E 3468 **Syntype**. **Type species** of *Echinasterella* Stürtz, 1890 : 225. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 225, pl. 28 figs 26, 26a,b.

E 3489 **Syntype**. **Type species** of *Echinasterella* Stürtz 1890: 225. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 225, pl. 28 fig. 27.

Echinasterias spinosus Stürtz
E 5000, E 5001 See: **Palaeosolaster gregoryi Stürtz**

Echinodiscus multidactylus Stürtz
E 4998, E 4999 See: **Palaeosolaster gregoryi Stürtz**

Echinostella traquairi Stürtz
E 4997 See: **Palaeosolaster gregoryi Stürtz**

Eoactis simplex Spencer

E 13154 **Holotype**. **Type species** of *Eoactis* Spencer, 1914 : 205. Silurian. Lower Ludlow, or Wenlock. Hafod, Llandovery, Dyfed, Wales. Morton, G. H. Colln. Purchd from Miss Morton July 1900. Type figd Spencer, W. K. (1914–1940) 1914: 30, pl. 1 fig. 4; 1922: 205–208, text figs 147, 148, pl.15 fig. 8.

G

Gasterometra polycirra Gislén
E 7401 See: **Stauranderaster** sp.

Girvanaster sculptus Spencer

E 52539 **Syntype**. **Type species**. **Lectotype** of *Protopalaeaster sculptus* (Spencer). Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1916: 61, 70, text figs 35, 72, pl.3 fig. 6. Type refd Owen, H. G. 1965: 568 as *Protopalaeaster sculptus* (Spencer). Selected by Owen as lectotype of species.

Goniaster (Astrogonium) coombii Forbes
OR 35503 See: **Nymphaster coombii (Forbes)**

Goniaster (Astrogonium) latus Forbes
OR 35504, OR 35505 See: **Calliderma latum (Forbes)**

Goniaster (Astrogonium) lunatus Woodward
E 5065 See: **Crateraster quinqueloba (Goldfuss)**

Goniaster (Astrogonium) smithiae Forbes
OR 75997 See: **Calliderma smithiae (Forbes)**

Goniaster (Astrogonium) smithii Forbes
OR 75997 See: **Calliderma smithiae (Forbes)**

Goniaster (Goniodiscus) bowerbankii Forbes
E 2578 See: **Metopaster bowerbankii (Forbes)**

Goniaster (Goniodiscus) mantelli Forbes
OR 76002, E 2570 See: **Metopaster mantelli (Forbes)**

Goniaster (Goniodiscus) parkinsoni Forbes
E 2569 See: **Metopaster parkinsoni (Forbes)**

Goniaster (Goniodiscus) rugatus Forbes
E 2585 See: **Metopaster rugatus (Forbes)**

Goniaster (Goniodiscus) uncatus Forbes
E 2577 See: **Metopaster parkinsoni (Forbes)**
OR 57518 See: **Metopaster rugatus (Forbes)**

Goniaster hamptonensis Wright
E 1066 See: **Calliderma hamptonensis (Wright)**

Goniaster mantelli Forbes
OR 76002, E 2570 See: **Metopaster mantelli (Forbes)**

Goniaster rugatus Forbes
E 2585 See: **Metopaster rugatus (Forbes)**

' . . . fragment of Goniaster sp. . . . '
E 2568 See: **Stauranderaster** sp.

Goniaster (Stellaster) comptoni Forbes
OR 34311 See: **Comptoniaster comptoni (Forbes)**

Goniaster stokesii Forbes
E 52239,44 See: **Teichaster stokesii (Forbes)**

Goniaster uncatus Forbes
OR 57518 See: **Metopaster rugatus (Forbes)**

Goniasteridae sp. A

E 54112 Cretaceous, Cenomanian. Grizzle, 2.66 m below datum. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 205, 207, pl. 43 figs 2a–c.

E 54358 (ex. 21029)(ex. Wright & Wright coll. No. 21029) Cretaceous, Cenomanian. Pit 2, Wilmington, Devon, England. C. W. & E. V. Wright Colln. Presd March 1977. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 205, 207, pl. 43 figs 1a–c.

Goniasteridae sp. B

E 54115 Cretaceous, Cenomanian. The White Hart Sand Pit, Wilmington, Devon, England. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 205, 207, pl. 43 figs 5a,b.

H

Hadranderaster abbreviatus (Spencer)

OR 57538 Holotype of *Pentaceros abbreviatus* Spencer. **Type species** of *Hadranderaster* Spencer 1907 : 125. Cretaceous. Upper Chalk. Charlton, Kent, England. Tennant, J. Colln. Purchd 16th November 1870. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 86–87, pl. 24 figs 1, 1a–c as *Pentaceros abbreviatus* Spencer; 1907: 125 referred to as *Hadranderaster abbreviatus* (Spencer).

Helianthaster filiciformis Woodward
E 13638, E 13639 See: **Devonistella filiciformis (Woodward)**

Helianthaster rhenanus Roemer

E 3361 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 218–219, pl. 26 figs 14a, 15 (fig. 15 is schematic with E 3362 and E 3363). Figd Spencer, W. K. (1914–1940) 1927: 372, 373, text fig. 237; 1930: 389, 390, 391, 392, text figs 249, 250.

E 3362 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 218–219, pl. 26 fig. 15 (fig. 15 is schematic with E 3361 and E 3363). Figd Spencer, W. K. (1914–1940) 1927: 373, 374, text fig. 240; 1930: 390.

E 3363 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 218–219, pl. 26 fig. 15 (fig. 15 is schematic with E 3361 and E 3362), pl. 27 fig. 14.

E 3513 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd 1894. Figd Stürtz, B. 1893: 12–13, pl. 1 fig. 4. Figd Spencer, W. K. (1914–1940) 1927: 372, 373, 387, text fig. 239, pl.24 fig. 9 (as E 3368); 1930: 390.

E 52860 Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, Rhineland, Germany. Stürtz, B. then Spencer, W. K. Colln. Presd Egerton, Mrs H. October 1955. Figd Spencer, W. K. (1914–1940) 1927: 372, 373; 1930: 390, 391, 392, text figs 238, 251.

Hippasteria tuberculata (Forbes)

E 52242 (ex. 57502) Eocene. London Clay. Isle of Sheppey, Kent, England. Bowerbank Colln 1850. Figd Rasmussen, H. W. 1972: 49, pl. 4 figs 5a,b.

E 53295 Eocene. London Clay. Foreshore, near Warden Point, Isle of Sheppey, Kent, England. Colld Sancto, R. G. Presd September 1963. Figd Rasmussen, H. W. 1972: 49, pl. 4 figs 2a,b.

OR 33832a,b Eocene. London Clay. Isle of Sheppey, Kent, England. Griffiths, W. Colln November 1854. Figd Rasmussen, H. W. 1972: 49, pl. 4 figs 3a,b (33832a), 4a–c (33832b) (both with 'E' prefix).

J

Jaekelaster petaliformis Stürtz
E 5003 See: **Compsaster petaliformis (Stürtz)**

L

Lepidactis wenlocki Spencer

OR 57476 Holotype. **Type species** of *Lepidactis* Spencer, 1918 : 113. Silurian. Wenlock Limestone. Dudley, Worcestershire, England. Allport, Samual Colln. Purchd 1871. Type figd Spencer, W. K. (1914–1940) 1918: 113–116, text figs 68–70, pl.6 fig.5.

Lepidaster grayi Forbes

OR 40215 Holotype. **Type species** of *Lepidaster* Forbes, 1850 : 1–2. Silurian. Wenlock Limestone. Quarries at Castle Hill, Dudley, Worcestershire, England. Gray, John Colln. Type figd Forbes, E. 1850a: 1–2, pl. 1 figs 1–3.

Linckia sp.

E 5055 (ex. 76002) Cretaceous. Lower Chalk. No locality data. Purchd Capron, J. R. 1879. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 100–101, pl. 27 figs 1, 1a.

Lophidiaster concavus Rasmussen

E 53630–31,33–34 Eocene, Ypresian. London Clay, division 3. Wraysbury Reservoir, Poyle, Buckinghamshire, England. Colld Rundle, A. J. & Cooper, J. Presd. Type figd Rasmussen, H. W. 1972: pl. 3 figs 20 (E 53630), 21 (E 53631), 23 (E 53633), 24 (E 53634).

E 53632 Holotype. Eocene, Ypresian. London Clay, division 5. Wraysbury Reservoir, Poyle, Buckinghamshire, England. Colld Rundle, A. J. & Cooper, J. Presd. Type figd

Rasmussen, H. W. 1972: 47–48, pl. 3 figs 22a,b.

E 53675 Eocene, Ypresian. London Clay, division 2. Aveley, Essex, England. Rundle, A. J. Colln. Type figd Rasmussen, H. W. 1972: pl. 3 fig. 25.

Lophidiaster pygmaeus Spencer

E 13263–4 **Syntypes**. Cretaceous, Upper Senonian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 139, 172, pl. 11 figs 20 upper (E 13263), lower (E 13264).

M

Mastaster sp.

E 54109 Cretaceous, Cenomanian. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 204, 207, pl. 43 figs 4a,b.

Mastaster villersensis Mercier

E 54096 Cretaceous, Cenomanian. Wilmington sands, 4.56m–9.4m below datum. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 203, 204, 207, pl. 43 figs 3a,b.

E 54106,7 Cretaceous, Cenomanian. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 200, 203, 204, pl. 42 figs 5a,b (E 54107), 7a,b (E 54107).

E 54169 Cretaceous, Lower Cenomanian. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 200, 204, pl. 42 figs 6a,b.

E 54370,1 (ex. Wright & Wright colln no. 2009, 2120) Cretaceous, Cenomanian. Hooken, Devon, England. Wright, C. W. & E. V. Colln. Presd March 1977. Figd Wright, C. W. & Wright, E. V. 1940: pl. 15 figs 2 left (E 54370), 2 right (E 54371). Figd Breton, G. 1979: 42, text fig. 24 (pars.).

E 54372 (ex. Wright & Wright colln no. 10414) Cretaceous, Cenomanian. sandy facies. Hooken, Devon, England. Wright, C. W. & E. V. Colln. Presd March 1977. Figd Wright, C. W. & Wright, E. V. 1940: 247, pl. 14 figs 14, 15, pl. 15 fig. 7.

E 54373 (ex. Wright & Wright colln no. 10414) Cretaceous, Cenomanian. Pit 2 Wilmington, Devon, England. Wright, C. W. & E. V. Colln. Presd March 1977. Figd Wright, C. W. & Wright, E. V. 1940: pl. 15 fig. 1.

E 54374 (ex. Wright & Wright colln no. 3535) Cretaceous, Cenomanian. Pit 2 Wilmington, Devon, England. Wright, C. W. & E. V. Colln. Presd March 1977. Figd Wright, C. W. & Wright, E. V. 1940: pl. 15 fig. 4. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 200, 203, pl. 42 fig. 3.

Mesopalaeaster complicatus Spencer

E 52445Aa,b,Ba,b **Holotype**. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Type figd Spencer, W. K. (1914–1940) E 52445Aa,b; 1916: 86–89, text figs 46, 47, 48; 1922: 226 ; E 52445Ba,b; 1916: 86–89, text fig. 47, pl.3 fig. 5; 1919: 179; 1922: 226. Figd Gale, A. S. 1987b: fig. 7G (E 52445Ab). The holotype is specimen E 52445Aa,b.

E 52504 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1916: 86–89, text fig. 46; 1919: 179; 1922: 226, pl. 2 fig. 9.

Mesopalaeaster primus Spencer

E 52441a,b **Syntype. Lectotype**. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Type figd Spencer, W. K. (1914–1940) E 52441a; 1916: 84–87, text fig. 44; 1919: 179, pl. 2 fig. 2; E52441b; 1916: 80, 84–87, text fig. 45; 1919: 179, pl. 3 fig. 8. Type refd Owen, H. G. 1965: 568. Selected by Owen as the Lectotype.

E 52542 **Syntype. Paralectotype**. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs R. Purchd 1920. Type refd Spencer, W. K. (1914–1940) 1916: 84–87.

Mesopalaeaster(?) leintwardinensis Spencer

E 13153 See: **Arisaigaster leintwardinensis (Spencer)**

Metopaster A

E 54367 See: **Metopaster** sp. A

Metopaster albocervus Gale

E 54287 **Paratype**. Cretaceous, Cenomanian. probably Wilmington Sands. The White Hart Sand Pit, Wilmington, Devon, England. Presd Gale, A. S. November 1988. Figd Gale, A. S. 1986: 21, pl. 9 fig. 15.

E 54288 **Holotype**. Cretaceous, Cenomanian. probably Wilmington Sands. The White Hart Sand Pit, Wilmington, Devon, England. Presd Gale, A. S. November 1988. Type figd Gale, A. S. 1986: 21, pl. 9 figs 16A–C.

Metopaster andraea Gale

E 54289 **Holotype**. Cretaceous, Cenomanian. The White Hart Sand Pit, Wilmington, Devon, England. Presd Gale, A. S. 1987. Type figd Gale, A. S. 1986: 22, pl. 9 figs 17A,B.

E 54290 **Paratype**. Cretaceous, Cenomanian. The White Hart Sand Pit, Wilmington, Devon, England. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: 22, pl. 9 figs 18A,B.

Metopaster bowerbankii Forbes

E 2578 See: **Metopaster bowerbankii (Forbes)**

Metopaster bowerbankii (Forbes)

E 2578 **Holotype** of *Goniaster* (*Goniodiscus*) *bowerbankii* Forbes. Cretaceous. Chalk. Kent, England. Bowerbank Colln. Type refd Forbes, E. 1848: 473 as *Goniaster* (*Goniodiscus*) *bowerbankii* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 333, pl. 22 fig. 4 as *Goniaster* (*Goniodiscus*) *bowerbankii* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 366, 370, 439, pl. 22 fig. 4 as *Goniaster* (*Goniodiscus*) *bowerbankii* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 42, 43, 45, pl. 16 figs 1a–c as *Metopaster bowerbankii* Forbes.

Metopaster bromleyi Gale

E 13304 **Syntype** of *Metopaster parkinsoni* (Forbes) var. *calcar* Spencer. **Holotype**. Cretaceous, uppermost Lower

Campanian. Trümmerkreide. Balsberg, North–east Skania, Sweden. Presd University of Lund. Type figd Spencer, W. K. 1913: 119–120, 176, pl. 15 fig. 13 as *Metopaster parkinsoni* (Forbes) var. *calcar* Spencer. Type refd Gale, A. S. 1986: 22, 24.

E 54192–4 Paratypes. Cretaceous, uppermost Lower Campanian. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 2 figs 14A,B (E 54192), 15A,B (E 54193), 16A,B (E 54194).

E 54341–6 Paratypes. Cretaceous, uppermost Lower Campanian. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 3 figs 1A,B (E 54341), 2A,B (E 54342), 3 left (E 54343), 3 right (E 54344), 4A,b (E 54345), 5 (54346).

Metopaster calcar Spencer

E 13305 Syntype of *Metopaster parkinsoni* (Forbes) var. *calcar* Spencer. **Lectotype**. Cretaceous, uppermost Lower Campanian. Trümmerkreide. Balsberg, North-east Skania, Sweden. Presd University of Lund. Type figd Spencer, W. K. 1913: 119–120, 176, pl. 15 figs 14–16 as *Metopaster parkinsoni* (Forbes) var. *calcar* Spencer. Type refd Gale, A. S. 1986: 24–25. Selected by Gale as the lectotype.

E 54245–67 Cretaceous, uppermost Lower Campanian. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: 24, pl. 8 figs 12A,B (E 54245), 13 (E 54246), 14A,B (E 54247), 15A,B (E 54248), 16A,B (E 54249), 17 (E 54250–63 in a group), 18 (E 54264), 19 (E 54265), 20 (E 54266), 21 (E 54267).

E 54270 Cretaceous, Santonian. Conglomerate horizon. Ringeleslätte, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 8 fig. 22.

Metopaster chilipora (Desmoulins)

E 34340 Cretaceous, Upper Campanian. Road cutting on the Autoroute de Charente, Gironde, Aquitaine, France. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 4 figs. 3A,B (not 2B as in plate explanation).

E 54218 Cretaceous, Upper Campanian. Talmont, near Royan, Charente, France. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 4 figs 1A,B.

E 54220 Cretaceous, Upper Campanian. Road cutting on the Autoroute de Charente, Gironde, Aquitaine, France. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 4 figs. 2A,B.

Metopaster cingulatus Sladen

OR 46776b Holotype. Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. 27th July 1869. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 53–55, pl. 14 figs 4a–d. The specimen was referred to by Sladen as bearing the registraton number 46776. This number is also carried by a specimen of *Metopaster uncatus* (Forbes), so the distinction is made by the suffixes a and b.

Metopaster cornutus Sladen

E 20723 Cretaceous, Turonian, *cuvieri* Zone. (with flints). Branscombe, South Devon, England. Rowe, A. W. Colln. Purchd November 1926. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: pl. 29 fig. 12.

Metopaster decipiens Spencer

E 20306 Holotype. Cretaceous, Campanian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Type figd Spencer, W. K. 1913: 118, 171, pl. 10 fig. 18. Figd Gale, A. S. 1986: 26–27, pl. 4 fig. 13.

Metopaster elegans Gale

E 54273, 75–6 Paratypes. Cretaceous, uppermost Lower Campanian. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: 28–29, pl. 8 figs 24A,B (E 54273); pl. 9 figs 2A,B (E 54275), 3A,B (E 54276).

E 54274 Holotype. Cretaceous, uppermost Lower Campanian. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Type figd Gale, A. S. 1986: 28–29, pl. 9 figs 1A,B.

Metopaster exsculptus Spencer

E 13021 (ex. E 2625) Cretaceous. Upper Chalk. England. Dixon, F. Colln. Figd Schulz, M.-G. & Weitschat, W. 1975: pl. 28 fig. 3 (referred to number 13021).

Metopaster hunteri (Forbes)

E 2583 Cretaceous. Upper Chalk. England. Old Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 60, 61, 62, pl. 12 figs 3a–e as *Mitraster hunteri* Forbes.

E 13058 Cretaceous. Upper Chalk. England. Hudson, R. Colln. Presd July 1907. Figd Gale, A. S. 1986: pl. 7 fig. 5.

E 13084 (ex. 46772) Cretaceous, Senonian. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. 1869. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 62, 67, pl. 9 figs 3a–e as *Mitraster hunteri* Forbes.

E 13279 Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 117, 172, pl. 11 fig. 2 as *Mitraster hunteri* Forbes.

E 20961–2 Cretaceous, Campanian, *mucronata* Zone. Isle of Wight, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 117, pl. 11 fig. 1 as *Mitraster hunteri* Forbes.

E 54225 Cretaceous, Santonian. basal lag of Phosphatic Chalk. Beauval, near Doullens, Somme, France. Gale, A. S. Colln. Presd 1987. Figd Gale, A. S. 1986: 30, pl. 7 figs 6A,B.

E 54226 Cretaceous, Lower Campanian. Phosphatic Chalk. Hallencourt pit, near Abbeville, Somme, France. Gale, A. S. Colln. Presd 1987. Figd Gale, A. S. 1986: 30, pl. 7 fig. 7.

E 54227 Cretaceous, Coniacian, 'pre- *coranguinum* Zone'. hardground. Hope Gap, north of Dieppe, France. Gale, A. S. Colln. Presd 1987. Figd Gale, A. S. 1986: 30, pl. 7 figs 8A,B.

OR 40274 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Simmons, J. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: pl. 15 figs 5a–b as *Mitraster hunteri* Forbes.

OR 40405 Cretaceous. Upper Chalk. Kent, England. Simmons, J. Colln. Figd Gale, A. S. 1986: pl. 17 fig. 1.

OR 46764 Cretaceous. Upper Chalk. Kent, England. Purchd Wood, J. 1868. Figd Gale, A. S. 1986: 30, pl. 7 fig. 4.

OR 46766a Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. January 1869. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 59, 61, 66, pl. 15 figs 3a–b as *Mitraster hunteri* Forbes. The specimen was referred to by Sladen as bearing the number 46766. This number is also carried by specimen of *Metopaster hunteri* (Forbes), so the distinction is made by suffixes a and b.

OR 46766b Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. January 1869. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 59, 61, pl. 15 figs 4a–d as *Mitraster hunteri* Forbes. The specimen was referred to by Sladen as bearing the number 46766. This number is also carried by another specimen of *Metopaster hunteri* (Forbes), so the distinction is made by suffixes a and b.

OR 46781 Cretaceous. Upper Chalk. Kent, England. Purchd Simmons, J. January 1870. Figd Gale, A. S. 1986: pl. 7 fig. 2.

OR 75539 Cretaceous. Upper Chalk. Bromley, Kent, England. Purchd Simmons, J. February 1864. Figd Gale, A. S. 1986: pl. 7 fig. 3.

Metopaster loirensis Gale

E 54207,9–14 Paratypes. Cretaceous, Santonian. Château Member, Craie de Villedieu, above glauconitized hardgrounds. Small roadside quarry between Villedieu and Le Trehet, Touraine, France. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: 31–32, pl. 3 figs 10 (E 54207), 12A,B (E 54208), 13 (E 54210), 14 (E 54211), 15 (E 54212), 16A,B (E 54213), 17 (E 54214). See remarks for E 54208.

E 54208 Holotype. Cretaceous, Santonian. Château Member, Craie de Villedieu, above glauconitized hardgrounds. Small roadside quarry between Villedieu and Le Trehet, Touraine, France. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: 31–32, pl. 3 figs 11A,B (referred to on p. 31 as E 54207, and in plate explanation as E 54208). Gale referred to E 54207 as the holotype on p. 31, but in the plate explanation he referred to E 54208 as the holotype. E 54208 is in fact the holotype because he referred to it as ' . . . a large ultimate superomarginal ossicle . . . ' on p. 31 and also in the plate explanation. E 54207 is referred to, in the plate explanation only, as ' . . . ultimate superomarginal . . . '.

E 54216 Cretaceous, Santonian. Craie de Villedieu, Calcarenites à bryozoaires de la Bouchardière. Villedieu Le Château, Touraine, France. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 3 figs 18A,B.

Metopaster mantelli Forbes

OR 40177, OR 76002, E 2570 See: **Metopaster mantelli (Forbes)**

Metopaster mantelli (Forbes)

E 2570 Cretaceous. Upper Chalk. No locality data. Bowerbank Colln. Figd Forbes, E. *in* Dixon, F. 1850: 332, pl. 23 fig. 11 as *Goniaster mantelli* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 366, 370, 440, pl. 23 fig. 11 as *Goniaster* (*Goniodiscus*) *mantelli* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 40, 41, pl. 13 figs 3a–b as *Metopaster mantelli* Forbes.

OR 40177 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Simmons, J. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 39, 40, 41, pl. 13 figs 2a–d as *Metopaster mantelli* Forbes.

OR 76002 Cretaceous. Upper Chalk. Gravesend, Kent, England. Bowerbank Colln. Figd Forbes, E. *in* Dixon, F. 1850: 332, pl. 23 fig. 12 as *Goniaster mantelli* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 366, 370, 440, pl. 23 fig. 12 as *Goniaster* (*Goniodiscus*) *mantelli* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 40, 41, pl. 13 figs 4a–b as *Metopaster mantelli* Forbes.

Metopaster parkinsoni Forbes

OR 40239, OR 40401, OR 46768, OR 46769, OR 46795, OR 46796, E 2034 See: **Metopaster parkinsoni (Forbes)**

OR 51413 See: **Metopaster uncatus (Forbes)**

Metopaster parkinsoni Forbes

OR 57528 See: **Metopaster uncatus (Forbes)**

Metopaster parkinsoni (Forbes)

E 2034 Cretaceous. Upper Chalk. Charlton, Kent, England. Purchd Harford, F. June 1888. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 33, 120, pl. 16 figs 2a–b as *Metopaster parkinsoni* Forbes.

E 2569 Lectotype. **Type species** of *Metopaster* Sladen 1893: 30. Cretaceous, (probably Santonian, high *coranguinum* Zone, according to Gale). Upper Chalk. Possibly Sussex, Southern England. Dixon, F. Colln. Figd Forbes, E. *in* Dixon, F. 1850: 331, pl. 21 fig. 8 as *Goniaster* (*Goniodiscus*) *parkinsoni* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 365, 370, 439, pl. 21 fig. 8 as *Goniaster* (*Goniodiscus*) *parkinsoni* Forbes. Refd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 30, as the type description of *Metopaster*. Type figd Gale, A. S. 1986: 18, pl. 1 fig. 6. Specimen chosen by Gale as lectotype.

E 2577 Cretaceous. Upper Chalk. No locality data. Dixon, F. Colln. Figd Forbes, E. *in* Dixon, F. 1850: 331, pl. 21 fig. 8 as *Goniaster* (*Goniodiscus*) *uncatus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 365, 370, 439, pl. 21 fig. 8 as *Goniaster* (*Goniodiscus*) *uncatus* Forbes.

E 13729 Cretaceous, Turonian, *Terebratulina* Zone. Tingey's Pit, Wouldham, Kent, England. Dibley, G. E. Colln October 1922. Figd Gale, A. S. 1986: pl. 1 fig. 4.

E 20425 Cretaceous, Campanian, *pilula* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Spencer, W. K. 1913: 171, pl. 10 fig. 6.

E 53685 Cretaceous, probably Lower Campanian. Southern England. Beckles Colln. Figd Gale, A. S. 1986: pl. 2 figs 6a–c.

E 54190 Cretaceous, Middle Cenomanian. bed 10 of the Lower Chalk. West of Dover, Kent, England. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 1 fig. 2.

E 54191 Cretaceous, Middle Cenomanian. bed 10 of the Lower Chalk. West of Dover, Kent, England. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 1 fig. 3.

OR 40239 Cretaceous. Upper Chalk. Bromley, Kent, England. Simmons, J. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 34, 36, pl. 10 fig. 1 as *Metopaster parkinsoni* Forbes.

OR 40401 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Simmons, J. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 36, pl. 11 figs 1a–c as *Metopaster parkinsoni* Forbes.

OR 46768 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. May 1868. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: pl. 10 figs. 3a–c as *Metopaster parkinsoni* Forbes.

OR 46769 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. June 1868. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 34, 35, 36, pl. 10 figs. 2a–d as *Metopaster parkinsoni* Forbes.

OR 46795 Cretaceous. Upper Chalk. Bromley, Kent, England. Purchd Simmons, J. April 1870. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: pl. 9 figs. 2a–c as *Metopaster parkinsoni* Forbes.

OR 46796 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. May 1868. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 36, 37, pl. 12 figs. 1a–e as *Metopaster parkinsoni* Forbes.

OR 48079 Cretaceous. Upper Chalk. Kent, England. Dixon, F. Colln. Figd Smith, A. B. *in* Murray, J. W. (editor) 1985: 181, pl. 7.6.3.

OR 79521 Cretaceous, Cenomanian. Lower Chalk. Kent, England. Presd Marsham, R. Figd Gale, A. S. 1986: 20, pl. 1 fig. 1.

Metopaster cf parkinsoni (Forbes)

E 54202–5 Cretaceous, Coniacian. lower part of Craie de Villedieu, Calcaires durs de la Ribochère. Villedieu Le Château, Touraine, France. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 3 figs 6 (E 54202), 7 (E 54203), 8 (E 54204), 9 (E 54205).

Metopaster parkinsoni (Forbes) var. calcar Spencer

E 13304 See: **Metopaster bromleyi Gale**

E 13305 See: **Metopaster calcar Spencer**

Metopaster quadratus Spencer

E 20264, E 20265 See: **Metopaster uncatus (Forbes)**

Metopaster rugatus (Forbes)

E 2584 Cretaceous. Upper Chalk. England. Old Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 64, pl. 16 fig. 4 as *Mitraster rugatus* Forbes.

E 2585 Syntype of *Goniaster* (*Goniodiscus*) *rugatus* Forbes. Cretaceous, Senonian. Upper Chalk. Southeast England. Dixon, F. Colln. Type refd Forbes, E. 1848: 471 as *Goniaster* (*Goniodiscus*) *rugatus* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: pl. 32 fig. 15 as *Goniaster rugatus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 440, pl. 23 fig. 15 as *Goniaster* (*Goniodiscus*) *rugatus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 64, 66, pl. 16 figs 5a–d as *Mitraster rugatus* Forbes.

E 13079 (ex. 76002) Cretaceous. Upper Chalk. Gravesend, Kent, England. Purchd Capron, J. R. 1879. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 66, pl. 16 figs 3a–b as *Mitraster rugatus* Forbes.

OR 57518 Cretaceous. Upper Chalk. Kent, England. Presd Tennant October 1868. Figd Forbes, E. *in* Dixon, F. 1850: pl. 23 fig. 14 as *Goniaster uncatus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 440, pl. 23 fig. 14 as *Goniaster* (*Goniodiscus*) *uncatus* Forbes.

Metopaster rugissimus Gale

E 54228 Holotype. Cretaceous, uppermost Lower Campanian. bioclastic gravels. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Type figd Gale, A. S. 1986: 34–35, pl. 7 fig. 19.

E 54229–34,36 Paratypes. Cretaceous, uppermost Lower Campanian. bioclastic gravels. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: 34, 35, pl. 7 figs 20A,B (E 54229), 21 (E 54230), 22 (E 54231), pl. 8 figs 1 (E 54232), 2 (E 54233), 3A,B (E 54234), 5 (E 54236).

E 54297 Paratype. Cretaceous, uppermost Lower Campanian. bioclastic gravels. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 8 fig. 4 (as E 54246). The registration number E 54246 is duplicated in pl. 8 figs 4 and 13. In order to avoid confusion, the specimen of pl. 8 fig. 4 has been re-registered as E 54297.

'Metopaster' sharpii (Wright)

OR 75792 Holotype of *Stellaster sharpii* Wright. Jurassic. Inferor Oolite, Durston Ironstone. Near Northampton, Northamptonshire, England. Colld Sharp, S. Acquired February 1875. Type figd Wright, T. (1863–1880) 1880: 165, pl. 20 as *Stellaster sharpii* Wright.

Metopaster sp.

E 54272 Cretaceous, uppermost Lower Campanian. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 8 fig. 23.

E 54367 See: **Metopaster** sp. A

Metopaster sp. A

E 54367 (ex. Wright & Wright colln No. 16571) Cretaceous, Cenomanian. Pit 1, Wilmington, Devon, England. Wright, C. W. & Wright, E. V. Colln. Presd March 1977. Figd Wright, C. W. & Wright, E. V. 1940: 238, text figs 9a–c as *Metopaster* sp. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 198, 200, pl. 42 figs 2a,b as *Metopaster* A.

Metopaster spenceri Nielsen

E 54223 Palaeocene, Lower Danian. North of Højerup, Stevn's Klint, Denmark. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: pl. 4 figs 4A,B.

Metopaster tamarae Gale

E 54238 Holotype. Cretaceous, uppermost Lower Campanian. bioclastic gravels. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Type figd Gale, A. S. 1986: 36, pl. 8 fig. 6.

E 54239–43 Paratypes. Cretaceous, uppermost Lower Campanian. bioclastic gravels. Ivö Klack, Skania, Sweden. Presd Gale, A. S. 1987. Figd Gale, A. S. 1986: 36, pl. 8 figs 7A,B (E 54239), 8 (E 54240), 9 (E 54241), 10 (E 54242), 11A,B (E 54243).

Metopaster thoracifer Geinitz

E 20955–8 Cretaceous, Turonian, *cuvieri* Zone. Branscombe, Devon, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 110, 171, pl. 10 figs 2 left (E 20955), right (E 20956), pl. 10 figs 3 left (E 20957), right (E 20958).

E 20959–60 Cretaceous, Turonian, *cuvieri* Zone. Branscombe, Devon, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 171, pl. 10 figs 12 left (E 20959), right (E 20960).

Metopaster tumidus Spencer

E 13265 Paratypes. Cretaceous, Upper Campanian, upper *muconata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 113, 175, pl. 14 fig. 1. Spencer wrote that the specimen was reconstructed from ' . . . ossicles washed out . . . ' of a Chalk sample. The reconstruction as figured by him has subsequently been dismantled, and the ossicles are now retained loose.

E 13266 Holotype. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 113–114, 176, pl. 15 fig. 1.

E 13267–8,70–72 Paratypes. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 113?; 171, pl. 10 fig. 8 (E 13272), 176, pl. 15 figs 2 (E 13271), 3 (E 13267), 4,6, (E 13268), 7 (E 13270).

E 13269 Paratype. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 113?, 176, pl. 15 fig. 5 as *Metopaster tumidus* Spencer (probably var. *radiatus*).

E 13273 Paratypes. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 113, 175, pl. 14 fig. 2. Fig. 2 is a reconstruction from several components.

Metopaster tumidus Spencer (probably var. radiatus)
E 13269 See: **Metopaster tumidus Spencer**

Metopaster uncatus Forbes
OR 35488, OR 35496, OR 46776a See: **Metopaster uncatus (Forbes)**

Metopaster uncatus (Forbes)

E 20264 Paratype of *Metopaster quadratus* Spencer. Cretaceous, Campanian, *quadratus* Zone. level b. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 97–99, text figs 1a–d as *Metopaster quadratus* Spencer.

E 20265 Holotype of *Metopaster quadratus* Spencer. Cretaceous, Campanian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 97–99, text figs 2a–d as *Metopaster quadratus* Spencer. Figd Gale, A. S. 1986: 43, pl. 6 fig. 4.

E 20269 Cretaceous, Santonian, *coranguinum* Zone. Micheldever, Hampshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Gale, A. S. 1986: 43, pl. 5 fig. 6.

OR 35488 Cretaceous. Upper Chalk. Kent, England. Taylor, H. W. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 50, 51, pl. 14 figs 1a,b as *Metopaster uncatus* Forbes.

OR 35496 Cretaceous. Upper Chalk. Kent, England. Old Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 49, pl. 11 figs 3a,b as *Metopaster uncatus* Forbes.

OR 46776a Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. 27th October 1869. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 48, 49, 50, pl. 14 figs 2a–d as *Metopaster uncatus* Forbes. A specimen of *M. cingulatus* Sladen also bears the same registration number. The distinction is made by the suffixes a and b.

OR 51413 Cretaceous. Upper Chalk. Near Bromley, Kent, England. No collection data. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 36, pl. 11 figs 2a–c as *Metopaster parkinsoni* Forbes.

OR 51414 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Presd Marquis of Northampton. Figd Wright, C. W. & Smith, A. B. 1987: 213, 214, pl. 47 fig. 7.

OR 57528 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Purchd Simmons, J. 30th October 1871. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: pl. 10 figs 4a–c as *Metopaster parkinsoni* Forbes 1907: 124 as *Metopaster uncatus* (Forbes).

Metopaster undulatus Spencer

E 13274 Holotype. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 118, 176, pl. 15 fig. 20.

E 13275–7 Paratypes. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 118, 119, 176, pl. 15 figs 21, 22 (E 13275), 23 (E 13276), 24, 24a (E 13277).

E 13278 Paratypes. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 118, 171, pl. 10 fig. 19. The figure is of a reconstructed margin with several ossicles.

Metopaster zonatus Sladen

E 2575 Syntype. Cretaceous. Upper Chalk. Near Bromley, Kent, England. Old Colln. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 45–47, pl. 12 figs 2a–c.

E 2606 Syntype? Cretaceous. Upper Chalk. England. Old Colln. Type refd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 45–47. This is possibly one of the specimens referred to by Sladen.

E 13028 (ex. E 150) **Syntype?** Cretaceous. Upper Chalk. England. Presd Bright, B. 1873. Type refd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 45–47. This is possibly one of the specimens referred to by Sladen.

OR 57570 Syntype? Cretaceous. Upper Chalk. Bromley, Kent, England. Purchd Simmons, J. February 1873. Type refd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 45–47. This is possibly one of the specimens referred to by Sladen.

OR 75550 Syntype? Cretaceous. Upper Chalk. Bromley, Kent, England. Purchd Simmons, J. August 1873. Type refd Sladen, W. P. & Spencer, W. K. (1891–1908) 1893: 45–47. This is possibly one of the specimens referred to by Sladen.

Mitraster hunteri Forbes
E 2583, E 13084, E 13279, E 20961–2, OR 40274, OR 46766a, OR 46766b See: **Metopaster hunteri (Forbes)**

Mitraster rugatus Forbes
E 2584, E 2585, E 13079 See: **Metopaster rugatus (Forbes)**

N

Nymphaster angustatus (Forbes)

E 2580 Cretaceous. Upper Chalk. No locality data. Bowerbank Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 23, 24, pl. 9 figs 1a–b as *Pycnaster angustatus* Forbes; 1907: 95 as *Pycinaster angustatus* Sladen.

Nymphaster coombii Forbes
E 3350, OR 35503, OR 46623 See: **Nymphaster coombii (Forbes)**

Nymphaster coombii (Forbes)

E 3349 (ex. 76002) Cretaceous, Cenomanian. Lower Chalk. Folkestone, Kent, England. No collection data. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 18, pl. 7 figs 2a–b as *Nymphaster? coombii* Forbes.

E 3350 (ex. 76002) Cretaceous, Cenomanian. Lower Chalk. Glynde, Sussex, England. No collection data. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 18, pl. 7 figs 3a–b as *Nymphaster coombii* Forbes.

E 13724 Cretaceous, Santonian, *coranguinum* Zone. Northfleet, Kent, England. Dibley, G. E. Colln 1922. Figd Schulz, M.-G. & Weitschat, W. 1975: 275, pl. 29 figs. 3,4 as *Chomataster coombii* (Forbes). Figd Gale, A. S. 1988 (1987a): 154, 157, 159, text figs 1D,E (as E 12734), pl. 4 fig. 4.

OR 35503 Holotype of *Goniaster* (*Astrogonium*) *coombii* Forbes. Cretaceous, Turonian, *cuvieri* Zone. Lower Chalk. Balcombe Pit, Amberley, Sussex, England. Colld Coombe, G. Dixon, F. Colln. Figd Forbes, E. 1848: 474 as *Goniaster* (*Astrogonium*) *coombii* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 334, pl. 23 fig. 6 as *Goniaster* (*Astrogonium*) *coombii*

Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 367, 368, 440, pl. 23 fig. 6 as *Goniaster* (*Astrogonium*) *coombii* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 16, 17, pl. 8 figs 1a,b as *Nymphaster coombii* Forbes.

OR 46623 Cretaceous, Cenomanian. Lower Chalk. Betchworth, Surrey, England. Purchd Simmons, J. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 17, pl. 7 figs 1a–e as *Nymphaster coombii* Forbes.

OR 48620 Cretaceous, Albian. Upper Greensand. Isle of Wight, England. Saxby, Rev. W. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: pl. 19 fig. 3 as *Nymphaster coombii* Forbes 1907: 123 as *Calliderma smithiae* (Forbes).

Nymphaster humilis (Schultz & Weitschat)

E 54301 Cretaceous, late Coniacian. 2m beneath Phosphatic Hardground. Hardvilliers, near Breteuil, Picardy, France. Gale, A. S. Colln. Figd Gale, A. S. 1988 (1987a): 161, pl. 2 fig. 5.

Nymphaster humilis (Schulz & Weitschat)

E 28407a,b Holotype. Cretaceous, Santonian, *coranguinum* Zone. North Foreland, Kent, England. Colld 1884. Rowe, A. W. Colln. Purchd November 1926. Figd Schulz, M.-G. & Weitschat, W. 1975: 275–276, pl. 29 figs. 1 (E 28407a), 2 (E 28407b) — both referred to under E 28407 as *Chomataster humilis* Schulz & Weitschat. Figd Gale, A. S. 1988 (1987a): 161, pl. 2 fig. 3 (E 28407a under E 28407).

Nymphaster marginatus Sladen

OR 35484 Holotype. Cretaceous, Santonian, *coranguinum* Zone. Upper Chalk. Near Bromley, Kent, England. Taylor, H. W. Colln. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 18–19, pl. 7 figs. 4a–b. Figd Rasmussen, H. W. 1950: 79, 83–84, text figs 6b?, 6g as *Chomataster marginatus* (Sladen). Figd Gale, A. S. 1988 (1987a): 159, 166, pl. 4 fig. 10. Since figuring by Sladen, some of the matrix has been removed from the specimen.

Nymphaster obtusus (Forbes)

OR 35481 Cretaceous, Senonian. Upper Chalk. Kent, England. Taylor, H. W. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 75, 76, pl. 22 figs 2, 2a as *Pentagonaster obtusus* Forbes.

OR 40400 Cretaceous, Senonian. Upper Chalk. Kent, England. Purchd Simmons, J. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 75, 76, pl. 22 figs 1, 1a, 1b as *Pentagonaster obtusus* Forbes.

E 5038 (ex. 48084) **Syntype** of *Oreaster obtusus* Forbes. **Lectotype**. Cretaceous, Senonian. Upper Chalk. Lancing, Sussex, England. Dixon, F. Colln. Refd Forbes, E. 1848: 468 as *Oreaster obtusus* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 330, pl. 21 fig. 12 left as *Oreaster obtusus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 364, 370, 439, pl. 21 fig. 12 left as *Oreaster obtusus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 75, 76, pl. 22 figs 3b–g as *Pentagonaster obtusus* Forbes. Type figd Gale, A. S. 1988 (1987a): 155 (as E 50838), 166, pl. 4 figs 7A–C. E 5038 and E 5039 were once joined together by matrix, but since figuring by Forbes, have been separated.

E 5039 (ex. 48084) **Syntype** of *Oreaster obtusus* Forbes. **Paralectotype**. Cretaceous, Senonian. Upper Chalk. Lancing, Sussex, England. Dixon, F. Colln. Refd Forbes, E. 1848: 468 as *Oreaster obtusus* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 330, pl. 21 fig. 12 right as *Oreaster obtusus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 364, 370, 439, pl. 21 fig. 12 right as *Oreaster obtusus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 75, pl. 22 fig. 3a as *Pentagonaster obtusus* Forbes. E 5038 and E 5039 were once joined together by matrix, but since figuring by Forbes, have been separated.

E 20273 Cretaceous, Campanian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum. Figd Gale, A. S. 1988 (1987a): 155, pl. 4 fig. 6.

E 20566 Cretaceous, Campanian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum. Figd Gale, A. S. 1988 (1987a): 155, pl. 4 fig. 9.

Nymphaster oligoplax Sladen

OR 40178 See: **Ophryaster oligoplax (Sladen)**

Nymphaster radiatus Spencer

E 375 See: **Spenceraster radiatus (Spencer)**

Nymphaster rugosus Spencer

OR 57516 See: **Spenceraster rugosus (Spencer)**

Nymphaster studlandensis (Schulz & Weitschat)

E 54300 Cretaceous, ?low Upper Campanian. Hallembaye, near Maastricht, Holland (Belgium, according to Gale). Gale, A. S. Colln. Figd Gale, A. S. 1988 (1987a): 163, pl. 5 fig. 1.

Nymphaster? coombii Forbes

E 3349 See: **Nymphaster coombii (Forbes)**

O

Onychaster flexilis Meek & Worthen

E 2686 Lower Carboniferous. Keokuk Group. Crawfordsville, Indiana, U. S. A. Braun, F. Colln. Purchd 1889. Figd Spencer, W. K. (1914–1940) 1925: pl.21 fig. 12; 1927: 339.

Ophidiaster? davidsoni de Loriol

E 53996 (ex. E 1499) **Holotype**. Jurassic, Portlandian. Boulogne-sur-Mer, France. Wright, T. Colln. Purchd Butler, F. H. May 1887. Type figd Loriol, P. de, *in* Loriol, P. de & Pellat, E. 1875: 293–294, pl. 26 figs 13, 14 as *Ophidiaster? davidsoni* Wright. Matrix was removed subsequent to figuring.

Ophidiaster? davidsoni Wright

E 53996 See: **Ophidiaster? davidsoni de Loriol**

Ophryaster magnus Spencer

E 13280 Holotype. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 130, 177, pl. 16 fig. 25.

E 13281–5 Paratypes. Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Type figd Spencer, W. K. 1913: 177, pl. 16 figs 20 (E 13281), 22 (E 13284), 24 (E 13283), 23?, 26 (E 13282), 27 (E 13285). E 13281 is a restored portion of a specimen and is formed from four ossicles.

Ophryaster oligoplax (Sladen)

OR 40178 Holotype of *Nymphaster oligoplax* Sladen. **Type species** of *Ophryaster* Sladen 1913 : 129–130. Cretaceous, Santonian, *coranguinum* Zone. Upper Chalk. Near Bromley, Kent, England. Simmons, J. Colln. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: 19–21, pl. 8 figs 3a,b as *Nymphaster oligoplax* Sladen. Type refd Spencer, W. K. 1913: 129–130.

Ophryaster sulcatus Sladen

E 54070 Cretaceous, Cenomanian. Wilmington Sands, 5.14–9.10m below datum. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 200, pl. 42 figs 1a,b.

Ophryaster sulcatus (Sladen)

E 5063 (ex. 75921) **Holotype** of *Tomidaster sulcatus* Sladen. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Dover, Kent, England. Presd Townsend, R. M. 1877. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1891: pl. 5 figs 1a–c as *Tomidaster sulcatus* Sladen; 1907: 123–124 as *Calliderma smithiae* (Forbes).

Oreaster bulbiferus Forbes

OR 48748 See: **Stauranderaster bulbiferus (Forbes)**

Oreaster coronatus Forbes

OR 35480 See: **Stauranderaster coronatus (Forbes)**

Oreaster obtusus Forbes

E 5038, E 5039 See: **Nymphaster obtusus (Forbes)**

Oreaster ocellatus Forbes

E 2571 See: **Valettaster ocellatus (Forbes)**

Oreaster pistilliferus Forbes

OR 57634, E 2564, E 5037 See: **Stauranderaster pistilliferus (Forbes)**

Oreaster sp.

E 2566 See: **Valettaster argus (Spencer)**

Ossicula of Asteriidae

E 13573–4 See: **'Astropecten'** sp.

P

Palaeaster caractaci Gregory

52857a,b See: **Siluraster caractaci (Gregory)**

Palaeaster caractaci Salter MS

E 52857a,b See: **Siluraster caractaci (Gregory)**

Palaeaster sp.

E 13952 See: **Urasterella ruthveni (Forbes) var. leintwardinensis Spencer**

Palaeasterina bonneyi Gregory

OR 40299a,b See: **Palasterina antiqua (Hisinger)**

Palaeosolaster gregoryi Stürtz

E 4364 Lower Devonian. Bundenbach, Germany. Krantz, F. Colln. Purchd 1899. Figd Spencer, W. K. (1914–1940) 1925: 238, 239, 240, pl. 18 fig. 2.

E 4997 **Holotype** of *Echinostella traquairi* Stürtz. **Type species** of *Echinostella* Stürtz 1899 : 233–235. Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Type figd Stürtz, B. 1900 (1899): 233–235, pl. 3 fig. 11, pl. 4 fig. 12 as *Echinostella traquairi* Stürtz.

E 4998 **Syntype A** of *Echinodiscus multidactylus* Stürtz. **Type species** of *Echinodiscus* Stürtz 1899 : 231–233. Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Type figd Stürtz, B. 1900 (1899): 231–233, pl. 3 figs 9, 10 as *Echinodiscus multidactylus* Stürtz.

E 4999 **Syntype B** of *Echinodiscus multidactylus* Stürtz. **Type species** of *Echinodiscus* Stürtz 1899 : 231–233. Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Type figd Stürtz, B. 1900 (1899): 231–233, pl. 3 figs 6–8 as *Echinodiscus multidactylus* Stürtz.

E 5000 **Syntype A** of *Echinasterias spinosus* Stürtz. **Type species** of *Echinasterias* Stürtz 1899 : 230. Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Type refd Stürtz, B. 1900 (1899): 230 as *Echinasterias spinosus* Stürtz.

E 5001 **Syntype B** of *Echinasterias spinosus* Stürtz. **Type species** of *Echinasterias* Stürtz 1899. Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Type figd Stürtz, B. 1900 (1899): 230–231, pl. 2 fig. 5 as *Echinasterias spinosus* Stürtz. Figd Spencer, W. K. (1914–1940) 1925: 238, 239, 240, text figs 173a,b.

E 5002 **Holotype. Type species** of *Palaeosolaster* Stürtz 1899 : 226. Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Type figd Stürtz, B. 1900 (1899): 226–229, pl. 2 figs 1–3. Figd Spencer, W. K. (1914–1940) 1925: 238, 239, 240, text fig. 172?

Palaeostella solida Stürtz

E 3485 **Holotype. Type species** of *Palaeostella* Stürtz, 1890: 230–231. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 230–231, pl. 31 figs 42, 43, 43a.

E 3724 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd 1894. Figd Stürtz, B. 1893: pl. 1 figs 5–8.

Palasterina antiqua (Hisinger)

OR 40299a,b **Holotype** of *Palaeasterina bonneyi* Gregory. Silurian. Lower Ludlow Shales. Church Hill, Leintwardine, Herefordshire, England. Old Colln. Type figd Gregory, J. W. 1899: 40299a: 349–350, text figs 1, 3a, pl. 16 fig. 2a; 40299b: 349–350, text figs 2, 3b, pl. 16 fig 2b as *Palaeasterina bonneyi* Gregory. Figd Spencer, W. K. (1914–1940) 1922: 222, 228, 229, 233, text fig. 169, pl. 16 fig. 1 (40299a); 222, 228, 229, 232, 233, text fig. 168, pl. 16 fig. 2 (40299b).

OR 40301 Silurian. Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Marston, A. Colln. 1862. Figd Spencer, W. K. (1914–1940) 1916: pl. 4 fig. 6 as *Palasterina primaeva* Forbes; 1922: 221, 222, 228, 229, 231, 232, 233, text fig. 158b.

Palasterina follmanni Stürtz

E 3469 **Syntype**. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 226–228, pl. 29 fig. 29.

E 3470 **Syntype. Lectotype**. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 226–228, pl. 29 figs 30, 30a (fig. 30a is reversed). Type refd Owen, H. G. 1965: 563. Selected as lectotype by Owen.

E 3471 **Syntype. Paralectotype**. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 226–228, pl. 29 fig. 29. E 3470 selected as lectotype by Owen; E 3471 is a syntype of Stürtz.

E 5004 Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, south slope of Hunsrück, Rhineland, Germany. Stürtz, B. Colln. Purchd June 1900. Figd Spencer, W. K. (1914–1940) 1922: 235; 1925: 237, pl. 20 fig. 1.

E 13625 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd April 1910. Figd Spencer, W. K. (1914–1940) 1922: 222, 235, 236, pl. 16 fig. 4; 1925: 237.

E 13626 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd April 1910. Figd Spencer, W. K. (1914–1940) 1922: 201, 222, 235, 236, pl. 16 fig. 7.

E 13629 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd April 23rd. 1910. Figd Spencer, W. K. (1914–1940) 1922: 201, 222, 235, 236, pl. 16 fig. 6.

E 13635 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd April 1910. Figd Spencer, W. K. (1914–1940) 1922: 222, 235, 236, text fig. 171, pl.16 fig. 3; 1925: 237; 1940: 508.

E 13636 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd April 1910. Figd Spencer, W. K. (1914–1940) 1922: 222, 235, 236, pl. 16 fig. 5; 1925: 237.

Palasterina primaeva (Forbes)

E 4991 Silurian. Lower Ludlow. Underbarrow, near Kendal, Westmoreland, England. Morris, J. Purchd 1867. Figd Spencer, W. K. (1914–1940) 1922: 185, 223, 224, pl.15 fig. 7.

Palasteriscus devonicus Stürtz

E 3466 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 223–225, pl. 28 figs 23, 23a, 23b, pl. 29 fig. 24.

E 3467 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd. Figd Spencer, W. K. (1914–1940) 1919: 170, 172, 174, 177, text fig. 119 (recorded on p. 177 as E 3407).

E 5026 Lower Devonian. Hunsrückshiefer. Bundenbach, near Birkenfeld, Rhineland, Germany. Stürtz, B. Colln. Purchd September 1902. Figd Spencer, W. K. (1914–1940) 1919: 177, possibly text fig. 122; 1922: pl. 14 fig. 4.

Pentaceros abbreviatus Spencer

OR 57538 See: **Hadranderaster abbreviatus (Spencer)**

Pentaceros bispinosus Spencer

OR 35482 See: **Stauranderaster bispinosus (Spencer)**

Pentaceros boysii Forbes

OR 46600, OR 48083 See: **Stauranderaster boysii (Forbes)**

Pentaceros bulbiferus Forbes

OR 40399, OR 48748, OR 40175, E 5040, E 5041, E 5042 See: **Stauranderaster bulbiferus (Forbes)**

Pentaceros coronatus Forbes

OR 35480, E 2562 See: **Stauranderaster coronatus (Forbes)**

Pentaceros ocellatus Forbes

E 5012 See: **Valettaster ocellatus (Forbes)**

Pentaceros pistilliferus Forbes

OR 57634, E 2564, E 5037 See: **Stauranderaster pistilliferus (Forbes)**

Pentaceros punctatus Spencer

E 2561 See: **Stauranderaster senonensis Valette**

Pentaceros sp.

OR 5514 See: **Pycinaster angustatus (Forbes)**

Pentagonaster megaloplax Sladen

OR 46779, E 2582, E 5064, E 5065 See: **Crateraster quinqueloba (Goldfuss)**

Pentagonaster obtusus Forbes

OR 35481, OR 40400, E 5038, E 5039, See: **Nymphaster obtusus (Forbes)**

Pentagonaster quinqueloba (Goldfuss)

OR 46779, E 2582, E 5064, E 5065 See: **Crateraster quinqueloba (Goldfuss)**

Pentagonaster robustus Spencer

OR 48085 See: **Pycinaster angustatus (Forbes)**

Pentagonaster robustus Spencer

OR 48085 See: **Pycinaster angustatus (Forbes)**

Pentasteria (Archastropecten) cotteswoldiae (Buckman)

E 1633 Jurassic, Bathonian. Stonesfield Slate. Eyeford, near Naunton, Gloucestershire, England. Wright, T. Colln. Purchd Butler, F. H. May 1887. Figd Wright, T. (1863–1880) 1863: 116–118, pl. 10 figs 1a–c as *Astropecten cotteswoldiae* Buckman.

E 1634 Jurassic, Bathonian. Stonesfield Slate. Eyeford, near Naunton, Gloucestershire, England. Wright, T. Colln. Purchd Butler, F. H. May 1887. Figd Wright, T. (1863–1880) 1863: 116–118, pl. 9 figs 3a–c as *Astropecten cotteswoldiae* Buckman.

E 1635 Jurassic, Bathonian. Stonesfield Slate. Eyeford, near Naunton, Gloucestershire, England. Wright, T. Colln. Purchd Butler, F. H. May 1887. Figd Wright, T. (1863–1880) 1863: 116–118, pl. 9 figs 1a,b as *Astropecten cotteswoldiae* Buckman.

E 1636 Jurassic, Bathonian. Stonesfield Slate. Eyeford, near Naunton, Gloucestershire, England. Wright, T. Colln. Purchd Butler, F. H. May 1887. Figd Wright, T. (1863–1880) 1863: 116, pl. 9 fig. 4 as *Astropecten cotteswoldiae* Buckman.

Pentasteria (Archastropecten) cotteswoldiae (Buckman) var. stamfordensis (Wright)

OR 75797 Holotype. Jurassic, Aalenian, *murchisonae* Zone. Inferior Oolite, Collyweston Slate. St. Martin parish, Stamford, Northamptonshire, England. Colld Sharp, S. 13th. April 1853. Acquired 1876. Type figd Wright, T. (1863–1880) 1863: 118–120, pl. 6 figs 1a,b as *Astropecten cotteswoldiae* var. *stamfordensis* Wright.

Pentasteria (Archastropecten) cotteswoldiae (Buckman) var. stonesfieldensis (Wright)

E 2588 Holotype. Jurassic, Bathonian. Stonesfield Slate. Oxfordshire, England. Johnson, J. R. Colln. Purchd 1845. Type figd Wright, T. (1863–1880) 1863: 121 as *Astropecten cotteswoldiae* var. *stonesfieldenses* Wright; pl. 8 fig. 2 as *Astropecten cotteswoldiae* var. *stonesfieldensis* Wright.

Pentasteria (Archastropecten) cf huxleyi (Wright)

E 28383 (ex. E 941) Jurassic. Great Oolite. 1205 feet down in borehole, near Richmond Bridge, Surrey, England. Presd Judd, J. W. July 1885. Figd Hess, H. 1955: 16, text fig. 7 as *Archastropecten* cf *huxleyi* (Wright).

Pentasteria (Archastropecten) huxleyi (Wright)

OR 33848 Holotype of *Astropecten huxleyi* Wright. **Type** species of *Archastropecten* Hess 1955 : 27. Jurassic, Bathonian, *discus* Zone. Forest Marble. Near Malmesbury, Wiltshire, England. Buy, W. Colln 1854. Type figd Wright, T. (1863–1880) 1863: 123–125, pl. 8 figs 1a–d as *Astropecten huxleyi* Wright. Type refd Hess, H. 1955: 27 as *Archastropecten huxleyi* (Wright).

Pentasteria (Archastropecten) lorioli (de Loriol)

E 1639 **Holotype** of *Astropecten lorioli* Wright. Jurassic, Portlandian. Boulogne-sur-Mer, France. Wright, T. Colln. Purchd Butler, F. H. May 1887. Type figd Loriol, P. de, *in* Loriol, P. de & Pellat, E. 1875: 292–293, pl. 26 fig. 12 as *Astropecten lorioli* Wright.

Pentasteria (Archastropecten) portlandicus (Hess)

E 13739 **Holotype** of *Archastropecten portlandicus* Hess. Jurassic, Portlandian, *pseudogigas* Zone. Basal shell bed of Portland Stone. West coast of Isle of Portland, Dorset, England. Colld Cunnington, R. H. Presd October 1925. Type figd Hess, H. 1955: 53–54, pl. 4 figs 4–6 as *Archastropecten portlandicus* Hess.

E 13740a Jurassic, Portlandian, *pseudogigas* Zone. Basal shell bed of Portland Stone. West coast of Isle of Portland, Dorset, England. Colld Cunnington, R. H. Presd October 1925. Type figd Hess, H. 1955: 53, 54, text figs 13–15 (E 13740) as *Archastropecten portlandicus* Hess.

Pentasteria (Archastropecten) procera Hess

E 5021 **Holotype**. Jurassic, Bajocian. Inferior Oolite, about 14 feet from surface of middle bed of Freestone. Guiting Power, 10 miles east of Cheltenham, Gloucestershire, England. Presd Burrows, H. W. 22nd March 1902. Type figd Hess, H. 1960a: 331–334, pl. 1.

Pentasteria (Archastropecten) wittsii (Wright)

E 1637 **Holotype** of *Astropecten wittsii* Wright. Jurassic, Bathonian. Stonesfield Slate. Eyeford, near Naunton, Gloucestershire, England. Colld Witts, Rev. E. F. Wright, T. Colln. Purchd Butler, F. H. May 1887. Type figd Wright, T. (1863–1880) 1863: 120–121, pl. 9 figs 2a,b as *Astropecten wittsii* Wright. According to a label written by L. Bairstow and stored with the specimen, E 1637 was filmed by the '. . .Shell Film Unit, 15th. Oct. 1957, for an educational film directed by H. van Calder.'.

Petraster kinahani (Baily)

E 194 Ordovician, Caradocian. Ballymoney Series. West of Ballymadden Point, near Bannow, County Wexford, Ireland. Purchd Baily, W. H. May, 1882. Figd Spencer, W. K. (1914–1940) 1916: 105, 106, text fig. 60 pl. 5 fig. 2.

E 13110a–d (ex. E 194) Ordovician, Caradocian. Ballymoney Series. West of Ballymadden Point, near Bannow, County Wexford, Ireland. Purchd Baily, W. H. May, 1882. Figd Spencer, W. K. (1914–1940) 1916: 105, 106, text fig. 61 (E 13110b, not E 13110a as stated in text); 1918: 109, 110, 146, pl. 5 figs 4 (E 13110d), 5 (E 13110a).

Phocidaster grandis Spencer

E 54361 (ex. Wright & Wright coll. no. 24631) Cretaceous, Cenomanian. bed 2. Pit 2, Wilmington, Devon, England. Wright, C. W. & E. V. Colln. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 197, 198, pl. 41 figs 4a,b.

Promopalaeaster elizae (Spencer)

E 52399a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1916: 96, 97 (E52399a); 92, 96, 97, text figs 57, 58 (E 52399b).

E 52404a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1916: 63, 92, 93, text fig. 51 (E 52404a); 95, pl. 4 fig. 5 (E 52404b).

E 52423a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1916: 67, 92, 93, 96, text figs 55, 56, pl. 4 fig. 3; 1919: 171 (E 52423a; counterpart E 52423b is not figured).

E 52478a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1916: 92, 93, 94, text fig. 53 (E 52478a); 92, 93, pl. 4 fig. 4 (E 52478b).

E 52588a,b **Holotype**. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1916: 63, 64, 92–97, text figs 51, 52, pl. 4 fig. 1; 1918: 146 (E 52588a); 1916: 92–97, pl. 4 fig. 2; 1919: 185 (E 52588b).

Protaster brisingoides Gregory

E 13000, E 13002 See: **Sturtzura brisingoides (Gregory)**

E 13001 See: **Sturtzura spryi Chapman**

Protopalaeaster ordovicus Spencer

E 52416a,b **Holotype**. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1916: 63, 73, 74, text fig. 36, pl.2 figs 6, 6a; 1919: 179 (E 52416a); 1916: 73, pl. 3 fig. 3; 1919: 179, 185 (E 52416b).

Protopalaeaster sculptus (Spencer)

E 52539 See: **Girvanaster sculptus Spencer**

Protopalaeaster sp

E 53918 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Presd June, 1937. Figd Gale, A. S. 1987b: fig. 7E.

Pycinaster angustatus (Forbes)

OR 5514 Cretaceous. Chalk. No locality data. Mantell, G. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 89, pl. 25 fig. 7 as *Pentaceros* sp. 1907: 95 as *Pycinaster angustatus* Sladen.

OR 48085 **Holotype** of *Pentagonaster robustus* Spencer. Cretaceous, Senonian. Upper Chalk. Sussex, England. Mantell, G. Colln 1853. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 73–74, pl. 21 figs 2, 2a as *Pentagonaster robustus* Spencer 1907: 95 as *Pycinaster angustatus* (Forbes). Spencer, 1907, revised his opinion as to the identity of the specimen when he wrote that it was '. . .probably an immature form. . .' of *P. angustatus*.

Pycnaster angustatus Forbes

E 2580 See: **Nymphaster angustatus (Forbes)**

Pycinaster angustatus Sladen

OR 5514 See: **Pycinaster angustatus (Forbes)**

Pycinaster crassus Spencer

E 2576 **Paratype**. Cretaceous. Upper Chalk. No locality data. Mantell, G. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 96, 97, pl. 29 fig. 1.

E 2628 **Paratype**. Cretaceous. Upper Chalk. England. Mantell, G. Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 96, pl. 29 fig. 5. This specimen has been lost.

E 2631a **Paratype**. Cretaceous. Upper Chalk. England. Bowerbank Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: pl. 29 figs 3, 3a (under E 2631).

E 2632a,b **Paratypes**. Cretaceous. Upper Chalk. England. Bowerbank Colln. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: pl. 29 figs 4 (E 2632a), 4a (E 2632b), (both under E 2632); 1908: 133.

E 13291–5 Cretaceous, Upper Campanian, upper *mucronata* Zone. Rügen, Germany. Purchd Laur, A. 27th October 1906. Figd Spencer, W. K. 1913: 177, pl. 16 figs 1, 3 (E 13291), 2 (E 13292), 125, pl.16 figs 4 (E 13293), 5 (E 13294), 6, 6a (E 13295).

OR 35498 **Holotype**. Cretaceous. Upper Chalk. Kent, England. Taylor, H. W. Colln. Purchd 1854. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 96–97, pl. 29 figs 2, 2a.

Pycinaster humilis Spencer

E 20963–4 **Paratypes**. Cretaceous, Turonian, *cuvieri* Zone. Branscombe, Devon, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 124, 172, pl. 11 figs 11 upper (E 20963), lower (E 20964).

Pycinaster magnificus Spencer

E 20424 Cretaceous, Campanian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 95, 96, pl. 29 fig. 6 as *Pycinaster senonensis* Valette.

E 20440–1 Cretaceous, Senonian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Wright, C. W. & Smith, A. B. 1987: 216, pl.47 figs 1 (E 20440), 2 (E 20441). The figures are reversed.

Pycinaster senonensis Valette

E 2561 See: **Stauranderaster senonensis Valette**
E 20424 See: **Pycinaster magnificus Spencer**
E 20431 See: **Stauranderaster senonensis (Valette)**

Pycinaster sp.

E 54036 Cretaceous, Cenomanian. lowest part of Wilmington Sands, 6.47–9.75m below datum. The White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Presd Gale, A. S. November 1988. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 195, 197, pl. 41 figs 3a,b (under E 54034).

Pycnaster angustatus Forbes and **Pycinaster angustatus Sladen**

E 2580 See: **Nymphaster angustatus (Forbes)**

R

Recurvaster blackmorei Rasmussen

E 13933 **Holotype**. Cretaceous, Campanian, *quadratus* Zone. level b. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Type figd Rasmussen, H. W. 1950: 64–66, pl. 6 figs 1–7. Figd Gale, A. S. 1986: 45, 47, pl. 9 fig. 5.

E 20275 Cretaceous, Campanian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Gale, A. S. 1986: 45, 47, pl. 9 figs 6A,B.

S

Schuchertia laxata (Schuchert)

E 52652 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1919: 177, 186, text fig. 126; 1922: 212, 218.

E 52698 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1922: 212, 213, text fig. 151, 214, pl.15 fig. 1.

E 52699 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1922: 212–214, text fig. 153.

E 52700 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1922: 212–214, text fig. 153.

Siluraster caractaci (Gregory)

E 52857a,b (ex. OR 48206) **Holotype** of *Palaeaster caractaci* Gregory. Ordovician, Caradoc. Caradoc Sandstone. Soudley Quarry?, Church Stretton, Shropshire, England. Colld Ketley, C. Purchd March 1867. Type refd Gregory, J. W. 1899: 344–345 as *Palaeaster caractaci* Salter MS. According to Gregory, 'The specimen . . . is contained in a small nodule, and is labelled from the Soudley Quarry. Mr. R. A. Buddacombe has . . . expressed doubt as to the exact correctness of this locality.' Figured herein, figs 1a,b.

Solaster moretonis Forbes

OR 40421 **Holotype**. Jurassic, Bathonian. Great Oolite, oolitic freestone. Windrush Quarry, Northleach, Gloucestershire, England. Colld Moreton, H. J., third Earl of Ducie. Presd 1863. Type figd Forbes, E. 1856: 1–3, pl. 1. Figd Wright, T. (1863–1880) 1863: 104–106, pl. 4 figs 1a–e.

Solaster murchisoni (Williamson)

E 13750 Jurassic, Pliensbachian, *capricornus* Zone. Lias, Starfish Bed. Huntcliff, east of Saltburn, Cleveland, England. Colld Crewdson, Canon G. Presd Kendal Borough Museum December 1926. Figd Blake, J. F. 1887: 529–531, pl. 15 figs 1, 2.

Spenceraster radiatus (Spencer)

E 375 **Holotype** of *Nymphaster radiatus* Spencer. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. South-east England. Gardner, J. Starkie Colln. Purchd 24th May 1884. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 73, pl. 25 figs 1a,b as *Nymphaster radiatus* Spencer.

E 13303 Cretaceous, Cenomanian, *varians* Zone. Near Cambridge, Cambridgeshire, England. Purchd Mockler, F. 28th October 1911. Figd Spencer, W. K. 1913: 131, 174, pl. 13 fig. 27 as *Trachyaster radiatus* Spencer.

Spenceraster rugosus (Spencer)

OR 57516 **Holotype** of *Nymphaster rugosus* Spencer. **Type species** of *Spenceraster* Lambert 1914 : 27. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Dover, Kent, England. Griffiths, W. Colln. Purchd. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 94, pl. 29 figs 7, 7a as *Nymphaster rugosus* Spencer. Type refd Lambert, J. 1914: 27.

Stauranderaster argus Spencer

E 2566, E 5019, E 20294 See: **Valettaster argus (Spencer)**

Stauranderaster bispinosus (Spencer)

OR 35482 **Holotype** of *Pentaceros bispinosus* Spencer. Cretaceous, Senonian. Upper Chalk. Sittingbourne, Kent, England. Taylor, H. W. Colln 1854. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 87, pl. 23 figs 3, 3a–c as *Pentaceros bispinosus* Spencer; 1907: 125 as *Stauranderaster bispinosus* (Spencer).

Stauranderaster boysii (Forbes)

OR 46600 Cretaceous. Upper Chalk. Near Bromley, Kent, England. Simmons, J. Colln. Purchd. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 80, pl. 22 figs 4, 4a–c as *Pentaceros boysii* Forbes 1907: 125 as *Stauranderaster boysii* (Forbes).

OR 48083 Cretaceous, Senonian. Upper Chalk. Bromley, Kent, England. Dixon, F. Colln 1850. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 80, pl. 23 figs 1, 1a,b as *Pentaceros boysii* Forbes; 1907: 125 *Stauranderaster boysii* (Forbes).

Stauranderaster bulbiferus Forbes

E 20965, E 20966 See: **Stauranderaster bulbiferus (Forbes)**

Stauranderaster bulbiferus (Forbes)

E 4344a Cretaceous. Chalk. Charlton, Kent, England. Ogle Colln. Purchd 27th June 1891. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 132, text fig. 34 (under E 4344). See also *Valettaster argus* (Spencer), E 4344b. The block of Chalk contains *S. bulbiferus* and *V. argus*.

E 5040 (ex. 48210) Cretaceous, Senonian. Upper Chalk. Bromley, Kent, England. Simmons, J. Colln *ca.* 1870. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 77–79, pl. 21 figs 1, 1a,b as *Pentaceros bulbiferus* Forbes; 1907: 125 as *Stauranderaster bulbiferus* (Forbes).

E 5041 (ex. 48210) Cretaceous, Senonian. Upper Chalk. Bromley?, Kent, England. Simmons, J. Colln. Purchd 1870. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 77, pl. 21 figs 3, 3a as *Pentaceros bulbiferus* Forbes; 1907: 125 as *Stauranderaster bulbiferus* (Forbes).

E 5042 (ex. 46765) Cretaceous, Senonian. Upper Chalk. Charlton, Kent, England. Simmons, J. Colln. Purchd 1878. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 77, pl. 23 figs 2, 2a as *Pentaceros bulbiferus* Forbes; 1907: 125 as *Stauranderaster bulbiferus* (Forbes).

E 20965 Cretaceous, Campanian, *mucronata* Zone. Isle of Wight, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 133, 134, pl. 13 figs 6, 7 as *Stauranderaster bulbiferus* Forbes.

E 20966 Cretaceous, Turonian, *cuvieri* Zone. Branscombe, Devon, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 133, pl. 13 fig. 8 as *Stauranderaster bulbiferus* Forbes.

OR 40175 Cretaceous, Senonian. Upper Chalk. Bromley, Kent, England. Simmons, J. Colln 1870. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 77, 79, pl. 20 figs 1a–c as *Pentaceros bulbiferus* Forbes; 1907: 125 as *Stauranderaster bulbiferus* (Forbes).

OR 40399 Cretaceous, Santonian, *coranguinum* Zone. Upper Chalk. Bromley, Kent, England. Charlesworth, E. Colln 1863. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 77, pl. 21 figs 4, 4a as *Pentaceros bulbiferus* Forbes; 1907: 125 as *Stauranderaster bulbiferus* (Forbes).

OR 48748 Cretaceous, Santonian, *coranguinum* Zone. Upper Chalk. Bromley, Kent, England. Simmons, J. Colln 1873. Figd Carpenter, P. H. 1882: 529–533, pl. 12 as *Oreaster bulbiferus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 77, 78, 79, pl. 20 figs 2, 2a–b as *Pentaceros bulbiferus* Forbes; 1907: 125 as *Stauranderaster bulbiferus* (Forbes). There are four other specimens on this slab, which altogether form an impressive display. However, they are attached to the slab by plaster of paris, with a steel bar inserted for strength, showing that the slab is composite, a sort of 'fake'.

Stauranderaster coronatus (Forbes)

E 2562 Cretaceous, Cenomanian. Lower Chalk. Burham, Kent, England. Smith, Mrs M. H. Colln 1878. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 82, 83, pl. 19 figs 1, 1a as *Pentaceros coronatus* Forbes; 1907: 125 as *Stauranderaster coronatus* (Forbes).

E 54031 Cretaceous, Cenomanian. lower part of Grizzle, 3.13 below standard datum. White Hart Sand Pit, Wilmington, Devon, England, SY 208 999. Gale, A. S. Colln. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 193, 194, 197, pl. 41 figs 2a,b.

OR 35480 **Holotype** of *Oreaster coronatus* Forbes. Cretaceous, Cenomanian. Lower Chalk. Washington, Sussex, England. Dixon, F. Colln 1850. Type figd Forbes, E. 1848: 467 as *Oreaster coronatus* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 327, 328, pl. 21 figs 7, 7a–e as *Oreaster coronatus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 362, 370, 439, pl. 21 figs 7, 7a–e as *Oreaster coronatus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 82, 83, pl. 24 figs 2, 2a–c, pl. 25 fig. 9 as *Pentaceros coronatus* Forbes; 1907: 125 as *Stauranderaster coronatus* (Forbes). Forbes, 1848, in his description of the species, referred to the figures in Dixon, 1850.

Stauranderaster gibbosus Spencer

E 13239 **Holotype**. Cretaceous, Upper Campanian, *quadratus* Zone. Rottingdean, Sussex, England. Presd Faber, H. 1913. Type refd Spencer, W. K. 1913: 135. Figured herein, figs 2a,b.

E 13240 **Paratype**. Cretaceous, Upper Senonian, *quadratus* Zone. Rottingdean, Sussex, England. Presd Faber, H. 1913. Figd Spencer, W. K. 1913: 135, pl. 13 fig. 11.

E 13248 Cretaceous, Senonian, lower quarter of *coranguinum* Zone. Whitchurch, Oxfordshire, England. Presd Withers, T. H. 25th September 1913. Figd Spencer, W. K. 1913: 133, 135, pl. 13 figs 1–3.

Stauranderaster pistilliferus (Forbes)

E 2564 **Syntype** of *Oreaster pistilliferus* Forbes. Cretaceous, Senonian. Upper Chalk. Gravesend, Kent, England. Old Colln. Figd Forbes, E. *in* Dixon, F. 1850: 329, possibly right–centre of pl. 21 fig. 15 as *Oreaster pistilliferus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 363, 370, possibly right–centre of pl. 21 fig. 15 as *Oreaster pistilliferus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 88, pl. 25 fig. 5 right as *Pentaceros pistilliferus* Forbes.

E 5037 (ex. 57634) **Syntype** of *Oreaster pistilliferus* Forbes. Cretaceous, Senonian. Upper Chalk. Bromley, Kent, England. Simmons, J. Colln 1873. Figd Forbes, E. *in* Dixon, F. 1850: 329, possibly left–centre of pl. 21 fig. 15 as *Oreaster pistilliferus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 363, 370, possibly left–centre of pl. 21 fig. 15 as *Oreaster pistilliferus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 88, pl. 25 fig. 5 left, as *Pentaceros pistilliferus* Forbes.

OR 57634 **Syntype** of *Oreaster pistilliferus* Forbes. Cretaceous, Senonian. Upper Chalk. Bromley, Kent, England. Simmons, J. Colln 1873. Figd Forbes, E. *in* Dixon, F. 1850: 329, probably upper right of pl. 21 fig. 15 as *Oreaster pistilliferus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 363, 370, probably upper right of pl. 21 fig. 15 as *Oreaster pistilliferus* Forbes. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 88, pl. 25 fig. 5 centre as *Pentaceros pistilliferus* Forbes.

Stauranderaster senonensis Valette

E 2561 **Holotype** of *Pentaceros punctatus* Spencer. Cretaceous, Senonian. Upper Chalk. 'England'. Old Colln. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 88, pl. 26 figs 1, 1a,b as *Pentaceros punctatus* Spencer; 1907: 95 as *Pycinaster senonensis* Valette.

Stauranderaster senonensis (Valette)

E 2561 See: **Stauranderaster senonensis Valette**

E 20431 Cretaceous, Campanian, *quadratus* Zone. East Harnham, near Salisbury, Wiltshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 96, 119, text figs 23a–c as *Pycinaster senonensis* Valette.

Stauranderaster sp.

E 2568 Cretaceous. Chalk. Sussex?, England. Old Colln. Figd Forbes, E. *in* Dixon, F. 1850: pl. 23 fig. 16 as '. . .fragment of *Goniaster* sp. . . .'. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: pl. 23 fig. 16 as '. . .fragment of *Goniaster* sp. . . .'.

E 7401 Cretaceous, probably Senonian. Devon, England. Bequest Vicary November 1903. Type figd Gislén, T. 1925: 28–30, figs 56–59 as *Gasterometra polycirra* Gislén. Refd Nielsen, K. B. 1943: 61. Erroneously described as a Comatulid crinoid by Gislén; referred to *Stauranderaster* by Nielsen.

Stellaster sharpii Wright

OR 75792 See: **'Metopaster' sharpii (Wright)**

Sturtzura brisingoides Gregory

E 13000, E 13002 See: **Sturtzura brisingoides (Gregory)**

Sturtzura brisingoides (Gregory)

E 13000 **Syntype** of *Protaster brisingoides* Gregory. **Lectotype** of *Sturtzura brisingoides* Gregory. **Type species** of *Sturtzura* Gregory, 1889 : 24–27. Upper Silurian. Melbournian Series, Mayhill Sandstone. Moonee Ponds, Flemington, near Melbourne, Victoria, Australia. Presd McKnight, F. 1889. Type figd Gregory, J. W. 1889: 24–27, text figs 1, 2 as *Protaster brisingoides* Gregory. Type refd Gregory, J. W. 1897 (for 1896): 1034–1035. Type figd Spencer, W. K. (1914–1940) 1927: 356, 363, 365, 366, text fig. 233B. E 13000 and E 13002 are part and counterpart.

E 13002 **Syntype** of *Protaster brisingoides* Gregory. **Lectotype** of *Sturtzura brisingoides* Gregory. **Type species** of *Sturtzura* Gregory, 1889. Upper Silurian. Melbournian Series, Mayhill Sandstone. Moonee Ponds, Flemington, near Melbourne, Victoria, Australia. Presd McKnight, F. 1889. Type refd Gregory, J. W. 1897 (for 1896): 1034–1035. Type figd Spencer, W. K. (1914–1940) 1927: 356, 362, 363, 365, 366, text fig. 232B. E 13000 and E 13002 are part and counterpart. E 13002 is not cited by Gregory 1889, although it is a syntype of *Protaster brisingoides* Gregory.

Sturtzura spryi Chapman

E 13001 **Syntype** of *Protaster brisingoides* Gregory. Upper Silurian. Melbournian Series, Mayhill Sandstone. Moonee Ponds, Flemington, near Melbourne Victoria, Australia. Presd McKnight, F. 1889. Type figd Gregory, J. W. 1889: 24–27, text fig. 3 as *Protaster brisingoides* Gregory.

T

Teichaster favosus Spencer

E 13238, E 13297–301 See: **Crateraster favosus (Spencer)**

Teichaster stokesii (Forbes)

E 52239,44 (ex. 57502) Eocene. London Clay. Isle of Sheppey, Kent, England. Bowerbank Colln 1850. Figd Forbes, E. 1852: pl. 4 figs 6a (E 52239, fig. reversed), 6b, 6c? (E 52244) as *Goniaster stokesii* Forbes.

OR 38587 Eocene. London Clay. Isle of Sheppey, Kent, England. Griffiths, W. Colln. Purchd October 1858. Figd Rasmussen, H. W. 1972: 53, pl. 12 fig. 5 (under E 38587).

Terminaster cancriformis (Quenstedt)

E 53615–17 Jurassic. Oxford Clay. Woodham Brick Pit, Buckinghamshire, England. Colld Beatson, S. Presd 4th June 1961. Figd Hess, H. 1974: 649, 650, text fig. 2 (E 53615); 648, 650, 651, text fig. 1 (E 53616); 649, 650, text fig. 3 (E 53617).

Tetraster sp

E 52383 See: **Cnemidactis girvanensis (Schuchert)**

Tholaster argus Spencer

E 20967 See: **Valettaster argus (Spencer)**

Tomidaster sulcatus Sladen

E 5063 See: **Ophryaster sulcatus (Sladen)**

Trachyaster radiatus Spencer

E 13303 See: **Spenceraster radiatus (Spencer)**

Tropidaster pectinatus Forbes

E 1861 **Syntypes? Type species** of *Tropidaster* Forbes 1850: 1–2. Jurassic, Pliensbachian, *capricornus* Zone. Lias. Cutting at south end of Mickleton Tunnel, near Chipping Campden, Gloucestershire, England. Colld Gavey, G. E. (civil engineer). Wright, T. Colln. Type refd Forbes, E. 1850c: 1–2, pl. 3. Figd Wright, T. (1863–1880) 1863: 102–103, pl. 3 fig. 1. These are probably some of the specimens referred to by Forbes in his description of the species and therefore may be syntypes.

E 1902 Jurassic, Pliensbachian, *capricornus* Zone. Lias. Cutting at south end of Mickleton Tunnel, near Chipping Campden, Gloucestershire, England. Colld Gavey, G. E. (civil engineer). Wright, T. Colln. Purchd Butler, F. H. April

1888. Figd Wright, T. (1863–1880) 1863: 102–103, pl. 3 fig. 3. These are not the specimens referred to by Forbes (1850) and are not syntypes. They were found subsequent to the description, as mentioned by Wright : 103.

E 13570 (ex. 75692) **Syntype? Type species** of *Tropidaster* Forbes 1850. Jurassic, Pliensbachian, *capricornus* Zone. Lias. Cutting at south end of Mickleton Tunnel, near Chipping Campden, Gloucestershire, England. Colld Gavey, G. E. (civil engineer). Purchd May 1875. Type refd Forbes, E. 1850c: 1–2, pl. 3. Perhaps amongst the specimens referred to by Forbes in his description of the species and therefore one of the syntypes.

OR 75690–1 Syntype. Type species of *Tropidaster* Forbes 1850 : 1–2. Jurassic, Pliensbachian, *capricornus* Zone. Lias. Cutting at south end of Mickleton Tunnel, near Chipping Campden, Gloucestershire, England. Colld Gavey, G. E. (civil engineer). Wright, T. Colln. Type figd Forbes, E. 1850c: 1–2, pl. 3 figs 1 (75960), 2,3 (75961).

Tropidaster tropidatus Forbes

OR 75692 Syntype? Jurassic, Pliensbachian, *capricornus* Zone. Lias. Cutting at south end of Mickleton Tunnel, near Chipping Campden, Gloucestershire, England. Colld Gavey, G. E. (civil engineer). Purchd May 1875. Type refd Forbes, E. 1850c: 1–2, pl. 3. Perhaps this is one of the specimens referred to by Forbes, and if so, it is one of the syntypes.

U

Uraster gaveyi Forbes

E 1638 See: **'Asterias' gaveyi (Forbes)**

Uraster spiniger Wright

E 1642 See: **Compsaster spiniger (Wright)**

Urasterella girvanensis Schuchert

E 52383 See: **Cnemidactis girvanensis (Schuchert)**

Urasterella mantana (Stschurowsky)

E 3806 Carboniferous. Mjatschowa, near Moscow, Russia. Purchd Damon, R. November 1896. Figd Spencer, W. K. (1914–1940) 1918: 122, 131, 147, 148, text fig. 93.

Urasterella ruthveni (Forbes) var. leintwardinensis Spencer

E 13952 Holotype. Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Ludlow Museum Colln. Purchd January 1947. Figd La Touche, J. de 1884: 76, pl. 17 fig 546 as *Palaeaster* sp. Type figd Spencer, W. K. (1914–1940) 1918: 127, 128, 130, 131, 138, 142–144, text fig. 92, pl. 9 figs 3, 4.

Urasterella thraivensis Spencer

E 52407Aa,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 127, 137–139, pl.10 fig. 1 (E 52407Aa); 137, 139 (E 52407Ab). E 52407A is referred to as *Urasterella girvanensis* on p. 303, and listed with *Encrinaster grayae* on p. 420 (1930).

E 52418a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 126–129, text fig. 81; E 52418a: 137, 139, 151.

E 52485 Lectotype. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 127, 128, 137, 139, text fig. 88, pl. 9 fig. 1. Type refd Owen, H. G. 1965. Selected by Owen to be the lectotype.

E 53290 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Colld Gray, Mrs. R. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1918: 127, 137–139, pl.9 fig.2.

V

Valettaster argus (Spencer)

E 2566 Paratype of *Stauranderaster argus* Spencer. Cretaceous. Chalk. Sussex, England. Dixon, F. Colln? Figd Forbes, E. *in* Dixon, F. 1850: pl. 21 fig. 16 as *Oreaster* sp. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 439, pl. 21 fig. 16 as *Oreaster* sp. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: pl. 25 figs 6, 6a, as Genus(?) sp.(?); 1907: 99, 100, pl. 29 figs 9, 9a as *Stauranderaster argus* Spencer.

Valettaster argus (Spencer)

E 4344b Cretaceous. Upper Chalk. Charlton, Kent, England. Ogle Colln. Purchd 27th June 1891. Figd Breton, G. 1985: 93, 99, fig. 7 (under E 4344). See also *Stauranderaster bulbiferus* (Forbes), E 4344a. The block of Chalk contains *S. bulbiferus* and *V. argus*.

E 5019 Holotype of *Stauranderaster argus* Spencer. Cretaceous, Campanian, *Marsupites* Zone. Brighton, Sussex, England. Presd McPherson, W. November 1901. Type refd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 99 as *Stauranderaster argus* Spencer.

E 20294 Paratype of *Stauranderaster argus* Spencer. Cretaceous, Santonian, *coranguinum* Zone. Micheldever, Hampshire, England. Blackmore, H. P. Colln. Presd Trustees, Salisbury Museum January 1935. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 99, 100, pl. 19 figs 8, 8a as *Stauranderaster argus* Spencer. Figd Breton, G. 1985: 93, fig. 6.

E 20967 Cretaceous, Santonian, *cortestudinarium* Zone. Seaford, Sussex, England. Rowe, A. W. Colln. Purchd November 1926. Figd Spencer, W. K. 1913: 138, pl. 13 fig. 23 as *Tholaster argus* Spencer.

Valettaster ocellatus (Forbes)

E 2571 Holotype of *Oreaster ocellatus* Forbes. **Type species** of *Valettaster* Lambert 1914 : 27. Cretaceous, Upper Senonian. Sussex, England. Dixon, F. Colln 1850. Type refd Forbes, E. 1848: 468 as *Oreaster ocellatus* Forbes. Figd Forbes, E. *in* Dixon, F. 1850: 329, pl. 21 fig. 13 as *Oreaster ocellatus* Forbes. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 364, 370, 439, pl. 21 fig. 13 as *Oreaster ocellatus* Forbes. Type refd Lambert, J. 1914: 27. Forbes 1848, in his description of the species, referred to the figures in Dixon 1850.

E 5012 Cretaceous, Upper Santonian. Upper Chalk, *Marsupites* Band. Between tide–marks, near Roedean College, Brighton, Sussex, England. Presd McPherson, W. 1901. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1905: 85, 86, pl. 25 figs 4, 4a as *Pentaceros ocellatus* Forbes. Figd Breton, G. 1985: 93, 98, fig. 5.

E 54359 (ex. Wright & Wright colln no. 2506) Cretaceous, Cenomanian. Pit 2, Wilmington, Devon, England. Wright, C. W. & E. V. Colln. Presd March 1977. Figd Gale, A. S., *in* Smith, A. B., Paul, C. R. C., Gale, A. S. & Donovan, S. K. 1988: 194, 197, pl. 41 figs 1a,b.

TYPE AND FIGURED FOSSIL OPHIUROIDEA

A

Acroura brodiei Wright
E 3769 See: **Sinosura brodiei (Wright)**

Amphiura cretacea Spencer
E 5059 **Holotype**. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Folkestone, Kent, England. Capron, J. R. Colln. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 104, 107, pl. 28 figs 6, 6a. The specimen is associated with a paratype of *Ophiotitanos tenuis* Spencer.

Amphiura prattii Forbes
OR 24682 See: **Ophiochiton? prattii (Forbes)**
OR 35607 See: **Dermocoma wrighti Hess**

Amphiura ?senonensis Valette
E 13696a,b Cretaceous, Campanian, *quadratus* Zone. Upper of two pits Patching Hill, Worthing, Sussex, England. Colld Gaster, C. T. A. Presd October 1921. Figd Rasmussen, H. W. 1950: 119, 120, pl. 15 figs 6, 7 (E 13696a), 8a–e (E 13696b) as *Amphiura ?senonensis* (Valette).

Amphiura ?senonensis (Valette)
E 13696a,b See: **Amphiura ?senonensis Valette**

Antiquaster magrumi Kesling
OR 40296b Silurian, Lower Ludlow. Shales. Church Hill, Leintwardine, Herefordshire, England. Marston, A Colln. Presd 1862. Figd Hotchkiss, F. H. 1976: 8, 9, 14, pl. 9 fig. 1.

Aplocoma sp
E 1613a,b(1–11) Triassic, Rhaetic. Spinney Hill, near Leicester, Leicestershire, England. Wright, T. Colln. Purchd Butler, F. H. 1887. Figd Hess, H. 1965: 169, 171, 173, text figs 9–20.

Aspidosoma grayae Spencer
E 52455a,b See: **Encrinaster grayae (Spencer)**

B

Bdellacoma vermiformis Salter
E 1259 Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Presd Lee, J. E. 1885. Figd Spencer, W. K. (1914–1940) 1940: 511, 512, 527, 528, 529, text figs 335D, 342A, pl. 36 fig. 4.
OR 40297 Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Old Colln. Figd Spencer, W. K. (1914–1940) 1940: 511, 512, 527, 528, 529, text figs 335C, 342B, pl. 37 fig. 8.

Belaster ordovicus Spencer
E 13532 See: **Stenaster obtusus (Forbes)**

Bundenbachia beneckei (Stürtz)
E 3461, 3494 See: **Taeniaster beneckei (Stürtz)**

Bundenbachia sp
E 3495 See: **Taeniaster beneckei (Stürtz)**

C

Caractacaster caractaci Gregory
E 13531a–c See: **Stenaster obtusus (Forbes)**

Cheiropteraster giganteus Stürtz
E 3464 **Syntype**. **Type species** of *Cheiropteraster* Stürtz 1890 : 228–229. **Lectotype**. Lower Devonian. Bundenbach Slates. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 228–229, pl. 29 fig. 33, pl. 30 fig. 32. Type figd Spencer, W. K. (1914–1940) 1934: 444, 445, 446, text fig. 287B. Selected by Spencer as the lectotype.
E 3465 **Syntype?** Lower Devonian. Bundenbach Slates. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1934: 439, 440, 441, 442, 444, 446, text figs 283A, 284, 286, 287A, pl. 29 fig. 4. The specimen may be a syntype of Stürtz.
E 3511 Lower Devonian. Bundenbach Slates. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1894. Figd Spencer, W. K. (1914–1940) 1934: 444, 445, 446, 447, 448, text figs 288, 289.

D

Dermocoma wrighti Hess
OR 35607 Jurassic, Bathonian. Forest Marble. Malmesbury, Wiltshire, England. Buy, W. Colln 1856. Figd Wright, T. (1863–1880) 1866: 158–159, pl. 18 fig. 2 as *Amphiura prattii* Forbes. Figd Hess, H. 1964: 789, 792, 796, pl. 10 fig. 2.

Drepanaster grayae Spencer
E 52402a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1934: 493 (E 52402a,b), pl.32 fig. 3 (E 52402a); 1940: 496, text fig. 323A (E 52402b).
E 52451a,b **Holotype**. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1934: 452, 475, 493; 1940: 495, 496, text fig. 322 (E 52451a); 1934: 493, 494, text fig. 321; 1940: 496, pl. 32 fig. 1 (E 52451b).
E 52461a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1934: 493 pl. 32 fig. 2 (E 52461b) (not fig. 3 as recorded in plate explanation. That specimen is E 52402a).
E 52495A,B Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1934: 493, pl. 32 fig. 4; 1940: 497 (E 52495A); 1934: 493; 1940: 497, 498, text fig. 325B,C (E 52495B).
E 52696 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1934: 493; 1940: 496, 497, text fig. 323B.
E 52767 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1940: 497, 498, text fig. 325A.
E 52939a,b Upper Ordovician, Ashgill. Ardmillan Series,

Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Presd Misses Gray June 1937. Figd Spencer, W. K. (1914–1940) 1940: 497, text fig. 324 (E 52939a).

Drepanaster scabrosus (Whidborne)

E 13121a,b Upper Devonian. Pilton Beds. Downend, near Saunton, North Devon, England. Presd Workman, Miss R. 29th July 1910. Figd Spencer, W. K. (1914–1940) 1934: pl. 29 fig. 6; 1940: 499 (E 13121a).

E 13737a,b Upper Devonian. Pickard's Down, near Barnstable, Devon, England. Colld Hamling, J. G. Presd October 1925. Figd Spencer, W. K. (1914–1940) 1940: 499, text fig. 326c.

E

Encrinaster grayae (Spencer)

E 52411a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 420, pl. 20 fig. 6 (E 52411a); 420, 423, pl. 26 fig. 7 (E 52411b).

E 52452a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 403, 410, 420, 421, 422, 423, text fig. 269, 271; 1934: 456 (E 52452a); 1930: 406, 420, text fig. 260, pl. 27 fig. 5; 1934: 450 (E 52452b).

E 52455a,b Holotype of *Aspidosoma grayae* Spencer. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1914: 23, 24, 25, 33, text figs 22, 24, pl. 1 fig.8; 1930: 403, 409, 410, 420, 421–423, text figs 259B, 269, 272, pl. 26 figs 1, 2, 3 (E 52455a); 1914: 23, 24, 25, 33, text figs 22, 24; 1930: 403, 409, 419, 420, 422, text figs 259A, 268, pl. 26 figs 1, 2, 4, pl. 28 fig. 4 (E 52455b) as *Aspidosoma grayae* Spencer.

E 52757 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 410, 420, 422, 424, text fig. 270.

Eospondylus primigenius (Stürtz)

E 3353 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1925: 257, 276, 310, 311, 312, text figs 206b, e, pl. 21 fig. 9.

E 3355 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 210–211, pl. 26 fig. 6 as *Ophiura* (*Ophiurella*) *primigenia* Stürtz. Figd Spencer, W. K. (1914–1940) 1925: 257, 276, 310, 311, 312, text figs 206c.

E 3357 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 210, pl. 26 fig. 7 as *Ophiura* (*Ophiurella) primigenia* Stürtz. Figd Spencer, W. K. (1914–1940) 1925: 257, 276, 310, 311, 312, text figs 206d.

E 3358 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1925: 257, 276, 310, 311, 312, text figs 206a. Figd Smith, A. B. *in* Murray, J. W. (editor) 1985: pl. 7.7.2.

Euzonosoma orbitoides Spencer

E 52424a,b Holotype. **Type species** of *Euzonosoma* Spencer 1930 : 411. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1930: 412, 413, 415, text fig. 264, pl. 27 fig. 9; 1934: 478 (E 52424a); 1930: 410, 411, 413, 414, text figs 265, 266, pl. 27 figs 6, 8 (E 52524b).

E 52426a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 412, 415 (E 52426a); 412, 415, 417, text fig. 267 (E 52426b).

E 52602a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 407, 410, 413, 415, 417, 423, text fig. 261 (both part and counterpart figd).

Euzonosoma tischbeinianum (Roemer)

E 3475 Lower Devonian. Bundenbach Slates. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1930: 407, 408, 417; 1934: 442; 1940: 501, text fig. 262.

E 13794 Lower Devonian. Bundenbach, Germany. Purchd Wolff, E. May 1935. Figd Smith, A. B. *in* Murray, J. W. (editor) 1985: pl. 7.7.1.

F

Furcaster leptosoma (Salter)

E 3351 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 213, pl. 26 figs 12, 13 as *Ophiura* (*Palastropecten*) *zitteli* Stürtz. Figd Spencer, W. K. (1914–1940) 1925: 313, 315, 319, 324, 325, pl. 22 fig. 7.

E 3352 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1925: 245, 313, 319, 325, pl. 22 fig. 8.

E 3354 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 211–213, pl. 26 figs 10, 10a, 11 as *Ophiura* (*Eoluidia*) *decheni* Stürtz. The specimen was used, together with E 3360, as the basis for the detailed reconstructions in the figures by Stürtz.

E 3360 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 211–213, pl. 26 fig. 10 as *Ophiura* (*Eoluidia*) *decheni* Stürtz. The specimen was used, together with E 3354, as the basis for the detailed reconstructions in the figures by Stürtz.

E 3364 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 214, pl. 31 fig. 40a as *Furcaster palaeozoicus* Stürtz. Figd Gregory, J. W. *in* Lankester, E. R. (editor) 1900: 275, text fig. 31. Stürtz based his figure on this specimen and E 3365. His figure was also used by Gregory.

E 3365 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 214, pl. 31 fig. 40a as *Furcaster palaeozoicus* Stürtz. Figd Gregory, J. W. *in* Lankester, E. R. (editor) 1900: 275, text fig. 31. Figd Spencer, W. K. (1914–1940) 1925: 314, 316, 319, 322, 324, text fig. 208. Stürtz based the figure on this specimen and E 3364. His figure was also used by Gregory.

E 3366 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 214, pl. 31

fig. 40 as *Furcaster palaeozoicus* Stürtz. Figd Spencer, W. K. (1914–1940) 1925: 313, 314, 319, 324, text fig. 207. Stürtz based his figure on this specimen and E 3805.

E 3487 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1925: 313, 319, 325, pl. 22 fig. 6.

E 3805 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Stürtz, B. 1890: 214, pl. 31 fig. 40 as *Furcaster palaeozoicus* Stürtz. Figd Spencer, W. K. (1914–1940) 1925: 319, 325, pl. 22 fig. 5. Stürtz based his figure on this specimen and E 3366. Gregory, 1897: 1038 referred to the specimen as the type, but the type series are in the Berlin Museum.

E 5036 **Holotype** of *Sympterura minveri* Bather. **Type species** of *Sympterura* Bather 1905: 168. Lower Devonian, 'Coblentian'. Blue slate. Ephaven Cove, between Lundy Beach and Trevan Point, Portquin Bay, St. Minver Parish, near Padstow, North Cornwall, England. Colld Legg, Miss B. Presd Fox, H. March 1905. Type figd Bather, F. A. 1905: 161–169, pl. 6 fig. 6 as *Sympterura minveri* Bather.

E 13698 Lower Devonian. Dachschiefer. Bundenbach, Hunsrückgebirge, Germany. Stürtz, B. Colln. Purchd 28th October 1922. Figd Spencer, W. K. (1914–1940) 1925: 313, 316, 319, 325, pl. 22 fig. 9.

E 20250a–c (ex. Ludlow Museum nos D/d/23 (=E 20250a), D/d/22 XXIII (=E 20250b), D/d/21 VII (=E 20250c)) Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Ludlow Museum Colln. Purchd January 1947. Figd Spencer, W. K. (1914–1940) 1925: 314, 316, 319, 320, 321, 322, text fig. 212c (E 20250c) as *Lapworthura miltoni* (Salter). Text fig. 212a, p. 321 is identified by its Ludlow Museum number III, which is in fact a specimen of *Lapworthura miltoni* (Salter), BMNH numbers E 20231–2. This is probably an error for VII, and if so, a further page reference will include text fig. 212a on p. 321.

E 20258 Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Ludlow Museum Colln. Purchd January 1947. Figd Spencer, W. K. (1914–1940) 1925: 316, 319, 321, 322, 325, text fig. 212e.

E 20260 Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Marston, A. Colln in Ludlow Museum Collection. Purchd January 1947. Figd Spencer, W. K. (1914–1940) 1925: 314, 319, pl. 18 fig. 4.

E 52839a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1925: 315, 317, 318, text fig. 210 as *Furcaster trepidans* Spencer; 1927: 325 (E 52839a) as *Furcaster leptosoma* (Salter).

Furcaster palaeozoicus Stürtz

E 3364, E3365, E 3366, E 3805 See: **Furcaster leptosoma (Salter)**

Furcaster trepidans Spencer

E 52413a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1925: 316, 317, pl. 22 fig. 1 (E 52413a).

E 52511 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1925: 315, 316, 317, text fig. 209.

E 52685a,b **Holotype** of *Squamaster trepidans* Spencer. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1925: E 52685a — 250, 290, text fig. 197c as *Squamaster trepidans* Spencer; 315, 317, as *Furcaster trepidans* Spencer; E 52685b — 250, 272, 273, 274, text fig. 192 as *Furcaster trepidans* Spencer; 290, text fig. 197c as *Squamaster trepidans* Spencer; 309, 313, 317, 318, pl. 22 fig. 2 as *Furcaster trepidans* Spencer.

Furcaster trepidans Spencer

E 52839a,b See: **Furcaster leptosoma (Salter)**

H

Hallaster cylindricus (Billings)

E 52394a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1925: 249, 251, 256, 257, 293, 295, text figs 178, 185, pl. 19 figs 1, 2, pl. 21 fig. 3; 1927: 335 (E 52394a); 1925: 249, 250, 251, 256, 257, 290, 291, 293, 295, 296, 315, text figs 178, 185, 197a, pl. 21 figs 1, 2; 1927: 335 (E 52394b).

E 52420a,b Ordovician, Caradoc. Balclatchie Group. Dow Hill, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1925: 246, 259, 265, 274, 292, 293, 295, 296, 315, text fig. 200; 1927: 325, 420; 1940: 524 (E 52420a).

E 52682 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1925: 251, 254, 293, 307, text fig. 179; 1930: 410.

Hemieuryale? lunaris Hess

E 52983–9 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss July 1896. Figd Hess, H. 1964: 763, 764, 765, text figs 4 (E 52983), 5 (E 52984), 6 (E 52985), 7 (E 52986), 8 (E 52987), 9 (E 52988), 10 (E 52989).

Hudsonaster batheri Schuchert

E 52391 See: **Stenaster obtusus (Forbes)**

L

Lapworthura miltoni (Salter)

E 20231–2 **Syntypes** of *Lapworthura sollasi* Spencer. Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Pardoe, H. & Ludlow Museum Colln of Collection. Purchd January 1947. Type figd Spencer, W. K. (1914–1940) 1914: 25, 31, 32, 33, 37, pl. 1 fig. 10 as *Lapworthura sollasi* Spencer; 1916: 106; 1918: 118; 1925: 302, 303 as *Lapworthura miltoni* (Salter). See also note for E 20250a–c, *Furcaster leptosoma* (Salter).

E 20235a,b **Neotype**. **Type species** of *Lapworthura* Gregory 1897: 1037. Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Ludlow Museum Colln. E 20235a, Purchd January 1947; E 20235b, Exchd Ipswich Museum per Spencer, H. E. P. 1964. Type refd Gregory, J. W. 1897 (for 1896): 1037. Type figd Spencer, W. K. (1914–1940) 1925: 302, 304–305, 309, pl. 20 fig. 2 (E

20235b). E 20235a was not referred to by Spencer. E 20235b was selected by Spencer, p.304, to be the 'holotype' in place of the original Salter specimen which was lost. The 'holotype' therefore is the neotype.

E 20250a–c See: **Furcaster leptosoma (Salter)**

E 52442a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1925: 302, 303, pl. 21 fig. 7 (E 52442a); 303, 309 (E 52442b).

E 52973a,b Silurian, Lower Ludlow. Quarry at Martins Shell, Leintwardine, Herefordshire, England. Spencer, W. K. ex Beale, A. R. Colln. Presd April 1964. Figd Spencer, W. K. (1914–1940) 1925: 302, pl. 20 fig. 3 (E 52973a).

E 52982 Silurian, Lower Ludlow. Quarry at Martins Shell, Leintwardine, Herefordshire, England. Spencer, W. K. Colln ex Beale, A. R. Collection. Presd April 1964. Figd Spencer, W. K. (1914–1940) 1925: 243, 256, 302, 305, 306, 308, text fig. 204C; 1927: 327.

OR 57425 Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Old Colln. Figd Gregory, J. W. 1897 (for 1896): 1037 fig. 5.

Lapworthura sollasi Spencer

E 20231–2 See: **Lapworthura miltoni (Salter)**

Loriolaster mirabilis Stürtz

E 3474 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1934: 439, 448, pl. 29 fig. 5.

E 3804 Lower Devonian. Bundenbach, Germany. Purchd Damon, R. March 1888. Figd Spencer, W. K. (1914–1940) 1934: 447, 448, text figs B,C.

E 13662a,b (ex. E 326) Lower Devonian. Dachschiefer. Bundenbach, Hunsrückgebirge, Germany. Purchd Braun, F. 1883. Figd Spencer, W. K. (1914–1940) 1934: 439, 447, 448, text figs 283B, 290A (E 13662a). Originally the two slabs containing the part and counterpart of E 13662a,b were numbered as E 326. Later on, they were given two registration numbers — E 13660 and E 13662. E 13660 contained one specimen plus the counterpart of E 13662, and E 13662 contained one specimen plus the counterpart of E 13660. To avoid confusion, suffixes a and b have been added to the specimens of each slab. Slab previously numbered E 13660 now contains E 13660a and E 13662b. Slab E 13662 now contains E 13662a and E 13660b.

E 13789 (ex. E 1029) Lower Devonian. Dachschiefer. Bundenbach, Hunsrückgebirge, Germany. Purchd Damon, R. 29th January 1886. Figd Spencer, W. K. (1914–1940) 1934: 439, 440, 441, 446, 448, text fig. 285.

M

Mastigactis aranea (Ruedemann)

E 52616a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 427, 428, text fig. 275A, pl. 28 fig. 8; 1940: 504 (E 52616a); 1930: 427, 429, text fig. 275B; 1940: 504 (E 52616b).

E 52621 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 427, 428, 429, pl. 28 figs 5, 6.

E 52690 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 427, pl. 28 fig. 7.

Medusaster parvus Whidborne

E 53296 **Holotype**. Upper Devonian. North–east of Harford Landkey, Devon, England. Hamling Colln. Presd Trustees, Torquay Museum November 1935. Type figd Whidborne, G. F. (1896–1907) 1898: 205–206, pl. 37 fig. 4.

Medusaster rhenanus Stürtz

E 3481 **Syntype**. **Type species** of *Medusaster* Stürtz 1890: 229–230. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 229–230, pl. 31 figs 34, 35.

E 3496–98 **Syntypes**. **Type species** of *Medusaster* Stürtz 1890: 229–230. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type refd Stürtz, B. 1890: 229–230. These are three of the four specimens referred to by Stürtz on page 229.

Miospondylus rhenanus (Stürtz)

E 3723 **Holotype**. **Type species** of *Miospondylus* Gregory 1897: 1039. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd 1894. Type figd Stürtz, B. 1893: 7–8, pl. 1 figs 1–3 as *Ophiura rhenana* Stürtz. Type refd Gregory, J. W. 1897 (for 1896): 1039. Figd Spencer, W. K. (1914–1940) 1925: 299–301, text fig. 202, pl. 21 fig. 6.

N

? var nana

E 2593 See: **Sturtzaster marstoni (Salter)**

O

Ophiochiton? prattii (Forbes)

OR 24682 Jurassic, Oxfordian. Oxford Clay. Chippenham, Wiltshire, England. Buy, W. Colln 1850. Figd Wright, T. (1863–1880) 1880: 158–159, pl. 18 figs 1a–d as *Amphiura prattii* Forbes. Figd Hess, H. 1964: 796–799, pl. 10 figs 1a–d.

Ophiocoma hessi Rasmussen

E 53635 **Holotype**. Eocene, Bartonian. Lower Barton Beds, Highcliffe Sands, horizon A3. Highcliffe-on-Sea, Hampshire, England. Colld Rundle, A. J. Presd. Type figd Rasmussen, H. W. 1972: 76–77, pl. 6 figs 6a–c.

E 53636 **Paratype**. Eocene, Bartonian. Lower Barton Beds, Highcliffe Sands, horizon A3. Highcliffe-on-Sea, Hampshire, England. Colld Rundle, A. J. Presd. Figd Rasmussen, H. W. 1972: 76–77, pl. 6 fig. 7.

Ophiocoma? nereida (Wright)

E 1065 **Holotype** of *Ophiurella nereida* Wright. Jurassic, Corallian. Calciferous Grit. Sandsfoot Castle, Weymouth, Dorset, England. Colld Buckman, Prof. J. Presd June 1886. Type figd Wright, T. (1863–1880) 1880: 156–157, text figs 39, 40 as *Ophiurella nereida* Wright. Figd Wright, T. 1882: 56–57, text fig. opposite p. 56 as *Ophiurella nereida* Wright. Figd Wright, T. 1886b: 53–55, text fig. on p. 54 as *Ophiurella nereida* Wright. The specimen has been damaged since figuring by Wright.

Ophiocoma? rasmusseni Hess
E 13734B Holotype. Cretaceous, Cenomanian. Lower Chalk, Grey Chalk. Dover, or Folkestone, perhaps Abbotscliff, about midway between Dover and Folkestone, Kent, England. Dibley, G. E. Colln. Purchd October 1922. Type figd Hess, H. 1960b: 747, 748, 752, 753–756, text figs 1B, 5–7.

Ophiocten? sp.
E 52997 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss July 1896. Figd Hess, H. 1964: 768, 771, text fig. 18.

Ophioderma gaveyi Wright
E 1640, E 2655 See: **Palaeocoma gaveyi (Wright)**

Ophioderma griesbachii Wright
E 1561, E 1615 See: **Ophiohybris griesbachii (Wright)**

'Ophioderma' tenuibrachiata Forbes
E 1641 Jurassic, Pliensbachian, *margaritatus* Zone. Middle Lias, Starfish Bed. Down Cliff, near Bridport Harbour, Dorset, England. Wright, T. Colln. Purchd Butler, F. H. 1887. Figd Wright, T. (1863–1880) 1866: 146, pl. 18 figs 5a–c.

Ophioglypha wetherelli (Forbes)
E 13702 See: **Ophiura wetherelli Forbes**

Ophiohybris griesbachii (Wright)
E 1561 Syntype of *Ophioderma griesbachii* Wright. **Lectotype**. Jurassic, Bathonian. Forest Marble. Oundle, Northamptonshire, England. Colld Griesbach, Rev. A. W. Wright, T. Colln. Purchd Butler, F. H. 1887. Type figd Wright, T. 1854: 378–380, pl. 13 figs 2a,b (figures reversed) as *Ophioderma griesbachii* Wright. Figd Wright, T. (1863–1880): 1866: 131, pl. 18 figs 3a,b, and possibly fig. 4; 1880: 155 as *Ophiurella griesbachii* Wright. Type refd Hess, H. 1964: 787. Hess referred to the specimen as the holotype, but as it is one of the figured syntypes of Wright, the specimen is in fact the lectotype.

E 1615 Syntype? of *Ophioderma griesbachii* Wright. Jurassic, Bathonian. Forest Marble. Oundle, Northamptonshire, England. Colld Griesbach, Rev. A. W. Wright, T. Colln. Purchd Butler, F. H. 1887. Type refd Wright, T. 1854: 378–380 as *Ophioderma griesbachii* Wright. This is probably one of the specimens from which the species was described by Wright. It is probably therefore an unfigured syntype.

E 52373 (ex. 56865) Jurassic. Great Oolite, Forest Marble. Oundle, Northamptonshire, England. Morris Colln. Figd Hess, H. 1964: 787, 788, pl. 5.

Ophiolepis murravii Forbes
E 1560, E 1859 See: **Ophiomusium murravii (Forbes)**

Ophiolepis ramsayi Wright
E 1862 See: **Ophiomusium? ramsayi (Wright)**

Ophiomusium murravii (Forbes)
E 1560 Jurassic. Middle Lias, [top Lower Lias]. Near Staithes, Coast of Yorkshire, England. Colld Murray, Dr. Wright, T. Colln. Purchd Butler, F. H. 1887. Figd Wright, T. (1863–1880) 1866: 151–152, pl. 14 figs 1a,b, pl. 19 fig 2 as *Ophiolepis murravii* Forbes.

E 1859 Jurassic. Middle Lias, [top Lower Lias]. Near Staithes, Coast of Yorkshire, England. Colld Murray, Dr. Wright, T. Colln. Purchd Butler, F. H. 1887. Figd Wright, T. (1863–1880) 1866: 151–152, pl. 17 figs 2a,b as *Ophiolepis murravii* Forbes.

Ophiomusium cf murravii (Forbes)
E 52990–93 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 765, 766, text figs 11 (E 52990), 12 (E 52991), 13 (E 52992), 14 (E 52993).

E 53001–2 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 765, 767, 769, text figs 22 (E 53001), 23 (E 53002).

Ophiomusium cf murravii (Forbes) or Ophiura? astonensis Hess
E 53014 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 773, 774, 775, text fig. 35.

Ophiomusium sp.
E 13734C Cretaceous, Cenomanian. Grey Chalk. Dover, or Folkestone, perhaps Abbotscliff, about midway between Dover and Folkestone, Kent, England. Dibley, G. E. Colln. Purchd October 1922. Figd Hess, H. 1960b: 747, 748, 756, text figs 1C, 8.

Ophiomusium weymouthiense (Damon)
E 1607a Jurassic. Oxford Clay. Weymouth, Radipole Backwater, or Ham Cliff, Dorset, England. Wright, T. Colln. Purchd Butler, F. H. 1887. Figd Hess, H. 1964: 782, pl. 2 fig. 2.

E 1607b Neotype. Jurassic. Oxford Clay. Weymouth, Radipole Backwater, or Ham Cliff, Dorset, England. Wright, T. Colln. Purchd Butler, F. H. 1887. Type figd Hess, H. 1964: 780–783, text fig. 41, pl. 4.

E 3500A Jurassic, Oxfordian. Weymouth, Radipole Backwater, or Ham Cliff, Dorset, England. Purchd Damon, R. Figd Hess, H. 1964: 782, pl. 3.

Ophiomusium? ramsayi (Wright)
E 1862 Syntype of *Ophiolepis ramsayi* Wright. Jurassic. Lower Lias, associated with *Isocrinus tuberculatus*. Down Hatherley, Vale of Gloucester, Gloucestershire, England. Wright, T. (ex Brodie, Rev. P. B.) Colln). Purchd Butler, F. H. April 1888. Type figd Wright, T. (1863–1880) 1866: 150–151, pl. 14 fig. 3 as *Ophiolepis ramsayi* Wright.

Ophiopetra bathonica Hess
E 52353 Holotype. Jurassic, Bathonian. Forest Marble. Chippenham, Wiltshire, England. Spath, L. F. Colln. Presd Spath, J. May 1957. Type figd Hess, H. 1964: 793–795, text figs 46–48, pl. 8.

Ophiotitanos laevis Spencer
E 5053 (ex. 57512) **Holotype**. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Dover, Kent, England. Purchd Griffiths, W. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 105, pl. 28 figs 3, 3a.

E 5058 (ex. 76004) Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Folkestone, Kent, England. Purchd Capron, J. R. 1879. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 104, 105, pl. 28 figs 4, 4a.

Ophiotitanos magnus Spencer
E 5060 (ex. 76004) **Holotype**. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Folkestone, Kent, England. Capron Colln. Purchd 1879. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 106, pl. 28 figs 5, 5a.

Ophiotitanos tenuis Spencer

E 5056 (ex. 76004) **Holotype**. **Type species** of *Ophiotitanos* Spencer 1907: 104. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Folkestone, Kent, England. Capron Colln. Purchd 1879. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 104–105, pl. 28 figs 1, 1a.

E 5057 (ex. 76004) **Paratype**. Cretaceous, Cenomanian, *subglobosus* Zone. Grey Chalk. Folkestone, Kent, England. Capron, J. R. Colln. Purchd 1879. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 104, pl. 28 figs 2, 2a.

E 13734A Cretaceous. Grey Chalk. Dover, or Folkestone, perhaps Abbotscliff, about midway between Dover and Folkestone, Kent, England. Dibley, G. E. Colln. Purchd October 1922. Figd Hess, H. 1960b: 747, 748, 749, 750, 751, text figs 1A, 2–4.

Ophiura bartonensis Rasmussen

E 52158 (ex. 33394) **Holotype**. Eocene, Bartonian. Barton Beds, Highcliffe Sands. Highcliffe-on-Sea, near Barton-on-Sea, Hampshire, England. Presd d'Urban, J. May 1854. Type figd Rasmussen, H. W. 1972: 68–70, pl. 9 fig. 2, pl. 14 fig. 2.

E 53651–2 Eocene, Bartonian. Barton Beds, horizon A3. Highcliffe-on-Sea, near Barton-on-Sea, Hampshire, England. Colld Rundle, A. J. Presd. Figd Rasmussen, H. W. 1972: pl. 9 figs 3a–d (E 53651), 4 (E 53652).

E 53653–7 Eocene, Bartonian. Middle Barton Beds, horizon E. Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Figd Rasmussen, H. W. 1972: pl. 9 figs 5 (E 53653), 6a–c (E 53654), 7a,b (E 53655), 8a,b (E 53656), 9a–c (E 53657).

E 53673–4 Eocene, Bartonian. Lower Barton Beds, horizon A3. Highcliffe-on-Sea, near Barton-on-Sea, Hampshire, England. Colld Rundle, A. J. Presd. Figd Rasmussen, H. W. 1972: pl. 14 figs 3 (E 53673), 4 (E 53674).

Ophiura bognoriensis Rasmussen

E 13761 Holotype. Eocene. London Clay, Starfish Bed. Bognor Regis, Sussex, England. Colld Venables, E. M. Presd March 1928. Type figd Rasmussen, H. W. 1972: 66–68, pl. 8 figs 1a–b.

E 53642–50 Paratypes. Eocene. London Clay, *Astarte* Bed (E 53642–46), Starfish Bed (E 53647–50). Bognor Regis, Sussex, England. Rundle, A. J. Colln. Figd Rasmussen, H. W. 1972: 67, pl. 8 figs 2a–c (E 53642), 3a–d (E 53643), 4 (E 53644), 5 (E 53646), 7a–c (E 53647), 8a,b (E 53648), 9a,b (E 53649), 10a–c (E 53650).

Ophiura carpelloides Rasmussen

E 53658 Holotype. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Type figd Rasmussen, H. W. 1972: 71–75, pl. 10 figs 1a–d.

E 53659–66 Paratypes. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Figd Rasmussen, H. W. 1972: 71, pl. 10 figs 2a,b (E 53659), 3a–c (E 53660), 4a,b (E 53661), 5 (E 53662), 6a,b (E 53663), 7a,b (E 53664), 8a,b (E 53665), 9a–c (E 53666).

Ophiura costata Rasmussen

E 53637 Holotype. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton Cliff, Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Type figd Rasmussen, H. W. 1972: 70–71, pl. 6 figs 8a–c.

E 53638 Paratype. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton Cliff, Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Figd Rasmussen, H. W. 1972: 70–71, pl. 6 figs 9a–c.

Ophiura davisi Rasmussen

E 53667 Paratype. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Figd Rasmussen, H. W. 1972: 75, pl. 10 figs 10a–c.

E 53668 Holotype. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Type figd Rasmussen, H. W. 1972: 75, pl. 10 figs 11a–c.

E 53669–72 Paratypes. Eocene, Bartonian. Middle Barton Beds, horizon E. Barton-on-Sea, Hampshire, England. Davis, A. G. Colln. Figd Rasmussen, H. W. 1972: 75, pl. 10 figs 12a–c (E 53669), 13a,b (E 53670), 14a,b (E 53671), 15a,b (E 53672).

Ophiura (Eoluidia) decheni Stürtz

E 3354, E 3360 See: **Furcaster leptosoma (Salter)**

Ophiura (Ophiurella) primigenia Stürtz

E 3355, E 3357 See: **Eospondylus primigenius (Stürtz)**

Ophiura (Palastropecten) zitteli Stürtz

E 3351 See: **Furcaster leptosoma (Salter)**

Ophiura parvisentis Spencer

E 5052 See: **Ophiura serrata Roemer**

Ophiura rhenana Stürtz

E 3723 See: **Miospondylus rhenanus (Stürtz)**

Ophiura serrata Roemer

E 5043 (ex. 48082) Cretaceous. Upper Chalk. Bromley, Kent, England. Dixon, F. Colln. Figd Forbes, E. *in* Dixon, F. 1850: 337, pl. 23 fig. 2. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: 369, 370, pl. 23 fig. 2. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 102, 103, pl. 27 figs 3, 3a.

E 5044 (ex. 48082) Cretaceous. Upper Chalk. Bromley, Kent, England. Dixon, F. Colln. Figd Forbes, E. *in* Dixon, F. 1850: pl. 23 fig. 3. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: pl. 23 fig. 3.

E 5045 (ex. 48082) Cretaceous. Upper Chalk. Bromley, Kent, England. Dixon, F. Colln. Figd Forbes, E. *in* Dixon, F. 1850: pl. 23 fig. 3a. Figd Forbes, E. *in* Dixon, F. & Jones, T. R. 1878: pl. 23 fig. 3a.

E 5046 (ex. 46778) Cretaceous, Santonian, *coranguinum* Zone. Chalk. Northfleet, Kent, England. Purchd Tennant, J. 1869. Figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 102, 103, pl. 27 figs 3b–e.

E 5052 (ex. 46776) **Holotype** of *Ophiura parvisentis* Spencer. Cretaceous, Senonian. Upper Chalk. Bromley, Kent, England. Purchd Simmons, J. 1869. Type figd Sladen, W. P. & Spencer, W. K. (1891–1908) 1907: 103–104, pl. 27 figs 4, 4a as *Ophiura parvisentis* Spencer. The specimen was recorded by Rasmussen, H. W. 1950: 113 as *Ophiura serrata* Roemer, and in a note included with the specimen he wrote ' . . . Ventral *side*. *O. parvisentum* must be a synonym . . . ', and dated 22/4/1948.

E 13733a,b Cretaceous, Santonian, *coranguinum* Zone. Northfleet, Kent, England. Dibley, G. E. Colln October 1922. Figd Rasmussen, H. W. 1950: 113, pl. 16 figs 1a–c (E 13733a), 2a–e (E 13733b).

Ophiura wetherelli Forbes

E 2650–52 Syntypes? Eocene. London Clay. Highgate Archway, North London, England. Presd Wetherell, J. W. 1871? Type refd? Forbes, E. 1852: 32–33. These specimens from the Wetherell Collection may be the ones referred to by Forbes on p. 32; if so, they are syntypes. E 2650 figured herein, fig. 5.

E 2670 Syntype. Eocene. London Clay. Highgate Archway, North London, England. Presd Wetherell, J. W. 1871. Type figd Forbes, E. 1852: 32–33 pl. 4 figs 7. Figd Busk, G. 1866: pl. 12 figs 4a–d. Although the original label reads ' . . . original figured specimen . . . ', the specimen does not resemble any figure by Forbes on pl. 4 figs 7, only that by Busk on pl. 12 fig. 4. Figured herein, fig. 4.

E 13702 Eocene. London Clay, division 4. Base of Norbiton Pottery Section, New Maldon, Surrey, England. Colld Davis, A. G. Presd December 1923. Figd Davis, A. G. 1923: 113–115, pl. 3 as *Ophioglypha wetherelli* (Forbes). Figd Rasmussen, H. W. 1972: 65, pl. 7 figs 2a,b, pl. 13 fig.3.

E 53243a,b Eocene, Ypresian. London Clay, 2 inches above the basal shell bed, of the Oldhaven Beds. Medway Brick and Sand Company, 'Arethusa Sand Pit', 200 yards west of pier at south end of Beacon Hill, Lower Upnor, Friendsbury Extra, Kent, TQ 759 712. England. Colld Members of the Ninth Symposium on Vertebrate Palaeontology and Comparative Anatomy September 1961. Presd October 1964. Figd Rasmussen, H. W. 1972: 65, pl. 7 fig. 1, pl. 13 fig. 2.

E 53639–41 Eocene. London Clay, division 2. Victoria Line shaft, Brixton, London, England. Rundle, A. J. Colln. Presd. Figd Rasmussen, H. W. 1972: 65, pl. 7 figs 3a–d (E 53639), 4 (E 53640), 5a,b (E 53641).

Ophiura? astonensis Hess

E 52994–5 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 766, 767, 768, text figs 15 (E 52994), 16 (E 52995).

E 52996 (ex. E 13085) **Holotype**. Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Type figd Hess, H. 1964: 767–768, text fig. 17.

Ophiura? astonensis Hess

E 53014 See: **Ophiomusium cf murravii (Forbes)**

Ophiura? substriata Rasmussen

E 13116 Holotype. Cretaceous, Lower Senonian. Chalk. Dover, Kent, England. Bequeathed Cockburn, C. F. 1909. Type figd Rasmussen, H. W. 1950: 116–118, pl. 18 figs 1–6.

Ophiurella griesbachii Wright

E 1561 See: **Ophiohybris griesbachii (Wright)**

Ophiurella nereida Wright

E 1065 See: **Ophiocoma? nereida (Wright)**

Ophiurina lymani Stürtz

E 3482 Syntype. **Lectotype**. **Type species** of *Ophiurina* Stürtz 1890: 232. Lower Devonian, Siegenian. Lower Hunsrückschiefer, Asterien–schiefer. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 232, pl. 31 figs 36, 36a. Type refd Owen, H. G. 1965: 558, 559, text fig. 349. Selected as lectotype by Owen, who also suggested the details of the stratigraphy.

E 3483(0–2) Syntypes. **Paralectotypes**. Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 232, pl. 21 fig. 37. Figd Spencer, W. K. (1914–1940) 1925: 284, 288, 289, text figs 196a,b, pl. 20 figs 7 (E 3483(1)), 8 upper (E 3483), lower (E 34832(2)). See also E 3482 which is the lectotype.

P

Palaeocoma egertoni (Broderip)

E 21 Jurassic. Lower Lias. Lyme Regis, Dorset, England. Purchd Executors of Tennant, J. June 1881. Figd Hess, H. 1960c: 780–781, text fig. 16.

E 204 Jurassic. Lower Lias. Lyme Regis, Dorset, England. Tennant Colln. Purchd May 1862. Figd Galopin, R., Lanterno, E. & Célébonovic, S. 1955: 60, pl. 40.

Palaeocoma gaveyi (Wright)

E 1640 Jurassic, Pliensbachian, *capricornus* Zone. Mickleton Tunnel, near Chipping Camden, Gloucestershire, England. Wright, T. Colln. Purchd Butler, F. H. May 1887. Figd Wright, T. (1863–1880) 1866: 147–148, pl. 15 fig. 1 as *Ophioderma gaveyi* Wright.

E 1903 Jurassic, Pliensbachian, *davoei* Zone, (according to Hess: 784). Middle Lias [top Lower Lias]. Mickleton Tunnel, near Chipping Camden, Gloucestershire, England. Wright, T. Colln. Purchd Butler, F. H. April 1885. Figd Hess, H. 1960c: 783, 784, 785, text figs 19a,b.

E 2655 Holotype of *Ophioderma gaveyi* Wright. Jurassic, Pliensbachian, *capricornus* Zone. 'Upper Shales of the Lower Lias'. Mickleton Tunnel, near Chipping Camden, Gloucestershire, England. Gavey, G. E. Colln 1880. Type figd Wright, T. 1854: 376–378, pl. 13 fig. 1 (figure is reversed) as *Ophioderma gaveyi* Wright. 'Collected by Mr. Gavey . . . whilst making the Oxford, Worcester and Wolverhampton Railway . . . ', (later to be part of the Great Western Railway). The specimen has been damaged since figuring.

E 52363 (ex. E 3342) Jurassic, *davoei* Zone. Lower Lias. Mickleton Tunnel and cuttings, Gloucestershire, England. Gavey Colln. Purchd Butler, F. H. March 1890. Figd Hess, H. 1960c: 783, 787, text figs 21a,b.

E 52364 (ex. E 3342) Jurassic, Pliensbachian, *davoei* Zone. Lower Lias. Mickleton Tunnel and cuttings, Gloucestershire, England. Gavey Colln. Purchd Butler, F. H. March 1890. Figd Hess, H. 1960c: 783, 786, 787, text figs 20a,b.

Palaeocoma milleri (Phillips)

E 53000 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 765, 769, text fig. 21.

E 53015 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 765, 774, text fig. 36.

E 53101–3 (ex. 19513) Jurassic, Pliensbachian. Kilsby Tunnel, Northamptonshire, England. Purchd Baker, Miss 1845. Figd Hess, H. 1964: 757, 759, 760, text fig. 1 (E 53101, fig. reversed); 758, 759, text fig. 2 (E 53102); 759, 761, text fig. 3 (E 53103).

E 53826 Jurassic, Pliensbachian. Middle Lias, Rock Bed. No locality data, ?England. No collection data. Figd Smith, A. B. *in* Murray, J. W. (editor) 1985: pl. 7.7.3.

Palaeophiura simplex Stürtz

E 3484 Holotype. **Type species** of *Palaeophiura* Stürtz 1890: 233. Lower Devonian. Bundenbach, Germany. Stürtz,

B. Colln. Purchd July 1891. Type figd Stürtz, B. 1890: 233, pl. 31 figs 38, 38a, 39. Figd Spencer, W. K. (1914–1940) 1940: 503, 504, text fig. 329.

Phragmactis grayae Spencer

E 52414a,b Holotype. **Type species** of *Phragmactis* Spencer 1940: 529–532. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Spencer, W. K. (1914–1940) 1940: 507–509, 513, 530–532, text figs 331A, 344, pl. 37 fig. 2 (E 52414a); 510, 532–534, text fig. 345, pl. 37 fig. 1 (E 52414b).

E 52494 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1940: 530, 532, 539, text fig. 343, pl. 37 fig. 3.

E 52614a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1940: 532, pl. 37 fig. 4 (E 52614a); 534 (E 52614b).

E 52941a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Presd Misses Gray June 1937. Figd Spencer, W. K. (1914–1940) 1940: 534, pl. 37 fig. 5 (E 54955a). Gray colln no. K99 was given in the plate explanation, but K98 was given on page 534.

Protaster piltonensis Spencer

E 13835a,b (ex. Torquay Museum nos 1291 (E 13835a), 1292 (E 13835b)) **Holotype**. Lower Carboniferous, Tournaisian, *Cleistopora* Zone, (according to Spencer 1934: 471 Upper Devonian *or* Lower Carboniferous, *Cleistopora* Zone). Top Orchard Quarry, Pilton, Devon, England. Presd Torquay Natural History Society per Milton, E. (curator) November 1936. Figd Whidborne, G. F. (1896–1907) 1898: 208–209, pl. 27 figs 2, 2a–c (E 13835a); 208–209, pl. 27 figs 1, 1a (E 13835b) as *Protaster? (Drepanaster) scabrosus* Whidborne var. Type figd Spencer, W. K. (1914–1940) 1934: 469–471 (E 13835a); 455, 469–471, text figs 303a, 304, pl. 33 fig. 1 (E 13835b).

Protaster salteri (Forbes)

E 13701 Near base of Upper Ordovician, Caradocian, *Mesograptus multidens* Zone, (according to Spencer: 469). Meadowtown Beds. Said to have been picked up from road near Rorrington, Shelve district, Shropshire, England. Colld Jones, J. Presd 13th August 1923. Figd Spencer, W. K. (1914–1940) 1934: 466, 468, 469, pl. 31 fig. 8.

Protaster? (Drepanaster) scabrosus Whidborne var

E 13835a,b See: **Protaster piltonensis Spencer**

R

Rhopalocoma pyrotechnica Salter

E 5013a,b Silurian, Lower Ludlow. Shales. Church Hill, Leintwardine, Herefordshire, England. Bather, F. A. Colln. Presd 1901. Figd Spencer, W. K. (1914–1940) 1940: 511, 512, 535, 536, 539, text figs 335E, 346, pl. 36 fig. 1 (E 5013a); 539, 540 (E 5013b). The reference to text fig. 345 on p. 512 is incorrect and should be text fig. 346.

OR 40293 Neotype. **Type species** of *Rhopalocoma* Salter 1857: 324–325. Silurian, Lower Ludlow. Shales. Church Hill, Leintwardine, Herefordshire, England. Marston, N. A. Colln. Type refd Salter, J. W. 1857: 324–325. Type figd Spencer, W. K. (1914–1940) 1940: 507, 509, 510, 513, 537–540, text figs 331D, 332, 347, 348, pl. 36 fig. 2.

S

Sinosura brodiei (Wright)

E 3769 Holotype of *Acroura brodiei* Wright. Jurassic, Pliensbachian, *capricornus* Zone. Middle Lias [top of Lower Lias]. Hewletts Hill, near Cheltenham, Gloucestershire, England. Purchd Brodie, Rev. P. B. October 1895. Type figd Wright, T. (1863–1880) 1866: 153, pl. 17 figs 5a–b (and probably fig. 5c, which is not referred to in the plate explanation, but is referred to on p. 153) as *Acroura brodiei* Wright.

E 52852a–e (ex. 18846n) Jurassic. Upper part of Lower Lias. Kilsby Tunnel, Northamptonshire, England. Purchd Baker, Miss 1845. Figd Hess, H. 1964: 775, 778, text fig. 37 (E 52852a); 775, 778, text figs 38–40 (E 52852b–d); 771, 778, pl. 1 (E 52852e).

E 52854A (ex. 19511) Jurassic. Upper part of Lower Lias. Kilsby Tunnel, Northamptonshire, England. Purchd Baker, Miss, 1845. Figd Hess, H. 1964: 777, pl. 2 fig. 1.

E 53003–6 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 770, text fig. 24 (E 53003); 770, text fig. 25 (E 53004); 770, 772, text fig. 26 (E 53005); 770, 772, text fig. 27 (E 53006).

E 53013 (ex. E 13085) Jurassic. Middle Lias. Aston Magna, Worcestershire, England. Slatter Colln. Purchd Slatter, Miss, July 1896. Figd Hess, H. 1964: 773–775, text fig. 34.

Squamaster trepidans Spencer

E 52685a,b See: **Furcaster trepidans Spencer**

Stenaster obtusus (Forbes)

E 13531a–c Upper Ordovician, Caradoc, Lower Bala, *Strophomena expansa* Zone. In lane to Gelli Grin Farmhouse, 2.5 miles southeast of Bala, Gwynedd, North Wales. Ruddy, T. Colln January 1915. Figd Spencer, W. K. (1914–1940) 1916: 80, 81, text fig. 42, pl. 3 fig. 7 (E 13531c); text fig. 43 (E 13531b); 84, 179, pl. 3 fig. 8 (E 13531a) as *Caractacaster caractaci* Gregory.

E 13532 Upper Ordovician, Caradoc, Lower Bala, *Strophomena expansa* Zone. In lane to Gelli Grin Farmhouse, 2.5 miles southeast of Bala, Gwynedd, North Wales. Ruddy, T. Colln January 1915. Figd Spencer, W. K. (1914–1940) 1916: 74, 75, 179, text fig. 37 pl. 3 fig. 4 as *Belaster ordovicus* Spencer.

E 52376 Syntype of *Tetraster wyvillethomsoni* Nicholson & Etheridge. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Nicholson, H. A. & Etheridge, R. 1880: 324–325, pl. 21 figs 7, 8 as *Tetraster wyville–thomsoni* Nicholson & Etheridge.

E 52377 Syntype of *Tetraster wyvillethomsoni* Nicholson & Etheridge. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Nicholson, H. A. & Etheridge, R. 1880: 324–325, pl. 21 figs 5, 6 as *Tetraster wyville–thomsoni* Nicholson & Etheridge.

E 52381a,b **Syntype** of *Tetraster wyvillethomsoni* Nicholson & Etheridge. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Nicholson, H. A. & Etheridge, R. 1880: 324–325, pl. 21 figs 3, 4 (E 52381a) as *Tetraster wyville–thomsoni* Nicholson & Etheridge. On the same block is a specimen figd by Nicholson & Etheridge, pages 328–330, pl. 22 fig. 12, as *Glyptocrinus* sp., no. E 69381a,b. E 69381a is the figured specimen of the crinoid.

E 52391 **Syntype** of *Tetraster wyvillethomsoni* Nicholson & Etheridge. **Holotype** of *Hudsonaster batheri* Schuchert. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type figd Nicholson, H. A. & Etheridge, R. 1880: 324–325, pl. 21 figs 1, 2 as *Tetraster wyville–thomsoni* Nicholson & Etheridge. Type figd Schuchert, C. 1915: 65, pl. 3 fig. 3 as *Hudsonaster batheri* Schuchert.

E 52398a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1914: 22, 23, 31, pl. 1 fig. 6; 1919: 173; 1927: 351, 354–356, text figs 225, 231B (E 52398b).

E 52400a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 347, 349, 356, 358, text fig. 223, pl. 23 figs 2,3 (E 52400a); 347, 349, 356, 358, text fig. 222, pl. 23 fig. 1 (E 52400b).

E 52409a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1914: 23, 31, 49, pl. 1 fig. 7; 1925: 263; 1927: 329, 352, 353, 355, 356, 358, 359, text figs 228A, 231A, pl. 24 fig. 10; 1930: 416 (E 52409a); 1927: 345, 353, 356, 358, 359, text fig. 229A, pl. 23 fig. 4 (but not pl. 26 fig. 4 as mentioned on page 356) (E 52409b).

E 52410a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Hotchkiss, F. H. 1976: 10, pl. 9 fig. 2 (E 52410b).

E 52431a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 353, 355, 356, 358, text fig. 230, pl. 23 fig. 6 (E 52431a).

E 52480a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 355, 356, text fig. 231c (E 52480b).

E 52486 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 345, 349, 350, 352, 354, 358, text fig. 224; 1934: 452, 453, text fig. 249A.

E 52570a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 351, 352, 353, 356, text fig. 229B; 1934: 470.

E 52571 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 353, 356, text fig. 229C.

E 52628 Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1927: 345, 356, text fig. 221.

E 54348 **Syntype** of *Tetraster wyvillethomsoni* Nicholson & Etheridge. Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Type refd Nicholson, H. A. & Etheridge, R. 1880: 324–325 as *Tetraster wyville–thomsoni* Nicholson & Etheridge.

Sturtzaster colvini (Salter)

E 13950 Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Ludlow Museum Colln. Purchd January 1947. Figd Spencer, W. K. (1914–1940) 1940: 521, 523, text fig. 340A.

E 20648 **Neosyntype** of *Sturtzaster colvini (Salter)*. Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Ludlow Museum Colln. Purchd January 1947. Figd Spencer, W. K. (1914–1940) 1940: 521, 523, text fig. 340B, pl. 35 fig. 2. Spencer chose two neotypes on p. 521. E 52859 was chosen by Owen, 1965: 547 as the neotype, so E 20648 is the neosyntype.

E 52859 **Neotype**. Silurian, Lower Ludlow. Church Hill quarry, Leintwardine, Herefordshire, England. Hawkins, H. L. Colln. Presd Department of Geology, Reading University, per Goldring, R. March 1964. Type figd Spencer, W. K. (1914–1940) 1940: 508, 509, 511, 512, 514, 515, 521, 522, 523, text figs 335B, 339, pl. 35 fig. 1, pl. 37, fig. 7. Type refd Owen, H. G. 1965: 547. Spencer chose two neotypes on p. 521. Owen selected E 52859 as the neotype. See also E 20648.

Sturtzaster marstoni (Salter)

E 2593 Silurian, Lower Ludlow. Shales. Church Hill, Leintwardine, Herefordshire, England. Holl, H. G. Colln. Purchd from his executors 1887. Figd Spencer, W. K. (1914–1940) 1940: 517, pl. 33 fig. 3 as? var *nana*.

E 13948 Silurian, Lower Ludlow. Church Hill, Leintwardine, Herefordshire, England. Pardoe, H. Colln. Purchd Ludlow Museum Collection January 1947. Figd Spencer, W. K. (1914–1940) 1940: 518, pl. 37 fig. 6.

Sturtzaster spinosissimus (Roemer)

E 13699 Lower Devonian. Dachschiefer. Bundenbach, Hunsrückgebirge, Germany. Stürtz, B. Colln. Purchd 25th November 1922. Figd Spencer, W. K. (1914–1940) 1940: 507, 511, 512, 513, 524, text figs 331B, 335A.

Sympterura minveri Bather

E 5036 See: **Furcaster leptosoma (Salter)**

T

Taeniaster beneckei (Stürtz)

E 3461 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1934: pl. 330 fig. 7 as1940: 503 as *Bundenbachia beneckei* (Stürtz).

E 3494 Lower Devonian. Bundenbach, Germany. Stürtz, B. Colln. Purchd July 1891. Figd Spencer, W. K. (1914–1940) 1940: 501, 502, text fig. 327 as *Bundenbachia beneckei (Stürtz)*.

E 3495 Lower Devonian. Bundenbach, Germany. Stürtz,

B. Colln. Purchd July 1891. Figd Gregory, J. W. 1897 (for 1896): 1034, text fig. 4 (based on the specimen) as *Bundenbachia* sp.

Taeniaster spinosus Billings

E 13120 Ordovician. Trenton Limestone. Belleville, Ontario, Canada. Purchd Smith, W. R. 1st March 1909. Figd Spencer, W. K. (1914–1940) 1925: 254; 1934: 485, 486, 488, text fig. 316.

E 13187 Ordovician, Trenton. Trenton Limestone. Belleville, Ontario, Canada. Purchd Smith, W. R. February 1909. Figd Spencer, W. K. (1914–1940) 1925: 254; 1934: 451, 454, 462, 474, 484–490, 497, text figs 292, 315, 317, 318, 319; 1940: 502.

Tetraster wyville–thomsoni Nicholson & Etheridge

E 52376, E 52377, E 52381a,b, E 52391, E 54348 See: **Stenaster obtusus (Forbes)**

Tetraster wyvillethomsoni Nicholson & Etheridge

E 52376, E 52377, E 52381a,b, E 52391, E 54348 See: **Stenaster obtusus (Forbes)**

U

Urosoma hirudo (Forbes)

E 13480 Lower Devonian, Siegenian, [recorded on label as Lower Coblentian]. Heiligenberg bei Oberstadtfeld, Eifel, Germany. Purchd Dohm, S. 23rd May 1914. Figd Spencer, W. K. (1914–1940) 1934: 437, 438, text figs 282B,C, pl. 29 fig.2.

E 13792 Lower Devonian, Gedinnian/Siegenian. *Orthis monieri* Beds. La Boë en Gahard, Ille et Vilaine, France. Original in the University of Rennes, Faculty of Science. Figd Spencer, W. K. (1914–1940) 1934: 438, pl. 29 fig. 3. The figured specimen is a wax squeeze.

E 52462a,b Upper Ordovician, Ashgill. Ardmillan Series, Drummuck Group, Starfish Bed. Thraive Glen, Girvan, Ayrshire, Scotland. Gray, Mrs R. Colln. Purchd 1920. Figd Spencer, W. K. (1914–1940) 1930: 436, text fig. 280; 1934: 437, text fig. 281 (E 52462a); 1930: 436, text fig. 279, pl. 27 fig. 3; 1934: 437, 438, text fig. 282A (E 52462b).

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INDEX OF SPECIES

[A] = Asteroid; [O] = Ophiuroid

abbreviatus, Hadranderaster [A]
——, *Pentaceros* **[A]**
acules, Chomataster [A]
albocervus, Metopaster [A]
andraea, Metopaster [A]
angustatus, Nymphaster [A]
——, Pycinaster [A]
——, *Pycnaster* **[A]**
antiqua, Palasterina [A]
aranea, Mastigactis [O]
argus, *Stauranderaster* **[A]**
——, *Tholaster* **[A]**
——, Valettaster [A]
armatus, *Astropecten* **[A]**
astonensis, Ophiura? [O]
(see also murravii, Ophiomusium)

bartonensis, Ophiura [O]
batheri, *Hudsonaster* **[O]**
bathonica, Ophiopetra [O]
beneckei, *Bundenbachia* **[O]**
——, Taeniaster [O]
bispinosus, *Pentaceros* **[A]**
——, Stauranderaster [A]
blackmorei, Recurvaster [A]
bognoriensis, Ophiura [O]
bonneyi, *Palaeasterina* **[A]**
bowerbankii, *Goniaster* (*Goniodiscus*) **[A]**
——, Metopaster [A]
boysii, *Pentaceros* **[A]**
boysii, Stauranderaster [A]
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brodiei, *Acroura* **[O]**
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——, Sinosura [O]
bromleyi, Metopaster [A]
bulbiferus, Coccaster [A]
——, *Oreaster* **[A]**
——, *Pentaceros* **[A]**
——, Stauranderaster [A]

calcar, Metopaster [A]
var. calcar, *Metopaster* **[A]**
cancriformis, Terminaster [A]

caractaci, *Caractacaster* [O]
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colei, Coulonia [A]
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——, var. stamfordensis, *Astropecten* [A]
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——, var. stonesfieldensis, *Astropecten* [A]
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——, *Aspidosoma* [O]
——, Drepanaster [O]
——, Encrinaster [O]
——, Phragmactis [O]
grayi, Lepidaster [A]
gregoryi, Palaeosolaster [A]
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——, Ophiohybris [O]
——, *Ophiurella* [O]

hamptonensis, Calliderma [A]
——, *Goniaster* [A]
hessi, Ophiocoma [O]
hirudo, Urosoma [O]
humilis, *Chomataster* [A]
——, Nymphaster [A]
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hunteri, Metopaster [A]
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——, *Astropecten* [A]
——, Pentasteria [A]
cf huxleyi, *Archastropecten* [A]
——, Pentasteria [A]

kinahani, Petraster [A]

laevis, ——, Ophiotitanos [O]
latum, Calliderma [A]
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——, *Mesopalaeaster(?)* [A]
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——, Ophiomusium [O]
cf murravii, Ophiomusium [O]
(see also astonensis, Ophiura?)

nereida, Ophiocoma? [O]
——, *Ophiurella* [O]

obtusus, Nymphaster [A]
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——, *Belaster* [O]
——, Protopalaeaster [A]

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pectinatus, Tropidaster [A]
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pyrotechnica, Rhopalocoma [O]
[* Crinoid]

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quinqueloba, Crateraster [A]
quinqueloba, *Pentagonaster* **[A]**

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——, Spenceraster [A]
——, *Trachyaster* **[A]**
var. radiatus, *Metopaster* **[A]**
(*see* **tumidus, Metopaster**)
ramsayi, *Ophiolepis* **[O]**
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rasmusseni, Ophiocoma? [O]
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rugissimus, Metopaster [A]
rugosus, *Nymphaster* **[A]**
——, Spenceraster [A]
ruthveni var. leintwardinensis, Urasterella [A]

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scabrosus, Drepanaster [O]
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simplex, Eoactis [A]
——, Palaeophiura [O]
sladeni, Echinasterella [A]
smithiae, Calliderma [A]
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substriata, Ophiura? [O]
sulcatus, Ophryaster [A]
——, *Tomidaster* **[A]**

tamarae, Metopaster [A]
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tenuis, Ophiotitanos [O]
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traquairi, *Echinostella* **[A]**
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——, *Squamaster* **[O]**
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tuberculata, Hippasteria [A]
tumidus (probably var. radiatus), Metopaster [A]
tumidus, Metopaster [A]

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——, *Goniaster* (*Goniodiscus*) **[A]**
——, Metopaster [A]
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villersensis, Mastaster [A]

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wittsii, *Astropecten* **[A]**
——, Pentasteria [A]
wrighti, Dermocoma [O]
wyville-thomsoni, *Tetraster* **[O]**
wyvillethomsoni, *Tetraster* **[O]**

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zonatus, Metopaster [A]

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Mobility and fixation of a variety of elements, in particular boron, during the metasomatic development of adinoles at Dinas Head, Cornwall

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C.T. WILLIAMS, R.F. SYMES and V.K. DIN

Department of Mineralogy, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

SYNOPSIS. A geochemical investigation of adinoles and related spilositic rocks from Dinas Head, Cornwall, has been undertaken in an attempt to clarify the relationship between these altered sediments and associated doleritic intrusions. Comparisons are made with other similar dolerite/sediment associations from northern Cornwall. Data for a wide range of major, minor and trace elements are presented for the various rock types observed, and the mobility, fixation and correlations for several elements during the adinolisation process discussed. Boron distribution maps, obtained by particle track analysis, and boron isotope ratios were used in an attempt to identify the potential source of the boron for the tourmalinisation of one suite of rocks in the area.

INTRODUCTION

As part of a programme to study mobility and fixation of trace elements during metasomatic (fluid) movement between igneous and associated sedimentary rocks, a geochemical study of the adinoles of the Dinas Head area, N. Cornwall has been made. This paper reports the results of this study.

Dinas Head is a small headland (GR SW 848,762), part of the Trevose Head promontory which lies some five miles west of Padstow on the north coast of Cornwall (Fig. 1). The area of Trevose Head (Dinas Head) is formed from a thick sequence of Upper Devonian sediments, mostly shales (now slates) and thinner carbonate-rich horizons. These beds were substantially deformed by Variscan earth movements so that some areas are extensively folded and faulted. However, despite this deformation, excellent thick series of spilosites and adinoles are exposed in the relatively steep cliffs of the headland, although no one band (or bed) of sediment can be traced with certainty into its metasomatised equivalent. Exposure is poor on the grass covered plateau at the top of the headland.

This sequence has been extensively intruded by massive dolerite sills, which form large 'greenstone' units at the base of the cliffs with minor stringers intruding parts of the rest of the sequence. The intrusion of these dolerites has been suggested as the cause of formation of the spilosites and adinoles of this area. The area has recently been remapped by a combined BGS/Exeter University team and will be published as 1:50,000 Geological Survey Sheet 335/336 (Trevose Head and Camelford).

BACKGROUND

The term adinole was first defined for rocks from the Harz Mountains of Germany by Kayser (1870) and first used for British rocks by Teall (1888) for rocks from the Tremadoc area of Wales. Often a crude relationship can be described such that the sequence adinole-spilosite-desmosite-unaltered shale represents increasing distance from contact with a basic igneous intrusion.

In the literature adinoles are usually described as massive, compact, featureless, white-weathering rocks consisting of a fine-grained mosaic of albite and quartz (often with minor carbonate). Spilosites have a distinctive 'spotted' texture and a fine-grained sericitic matrix, with chlorite and quartz, while desmosites, although formed from the same minerals as spilosites, tend to be banded rather than spotted.

The albite-rich rocks developed between the dolerite (greenstone) and shales of Dinas Head were first recognised as possible adinoles by Fox (1895). He questioned whether the soda-feldspar rocks (as he described them) were meta-igneous, and not metasediments, being originally keratophyric lavas or tuffs. However, he described spherulitic structures seen in one outcrop as apparently of igneous origin but concluded that they were metasomatised sediments. McMahon and Hutchings (1895) believed the spherulitic structure developed in the adinoles at Dinas Head to be a product of contact metamorphism. Dewey (1915) considered that the composition of the slate into which the dolerites were intruded affects the products of such metamorphism/metasomatism. He suggested that the iron content (and thus colour) of the original shales determines whether they become adinoles or not — such that purple, red or green shales (slates) rich in iron tend to develop spots (spilosites) but not as adinoles, and that the grey and black slates (poor in iron) do not develop spots but are strongly adinolised.

Agrell (1939, 1941) provided a very detailed petrographic and mineralogical study, with some chemical analyses, of the adinoles from Dinas Head and reported tourmaline to be locally abundant. He also pointed out the similarity of mineralogical and chemical composition between adinoles

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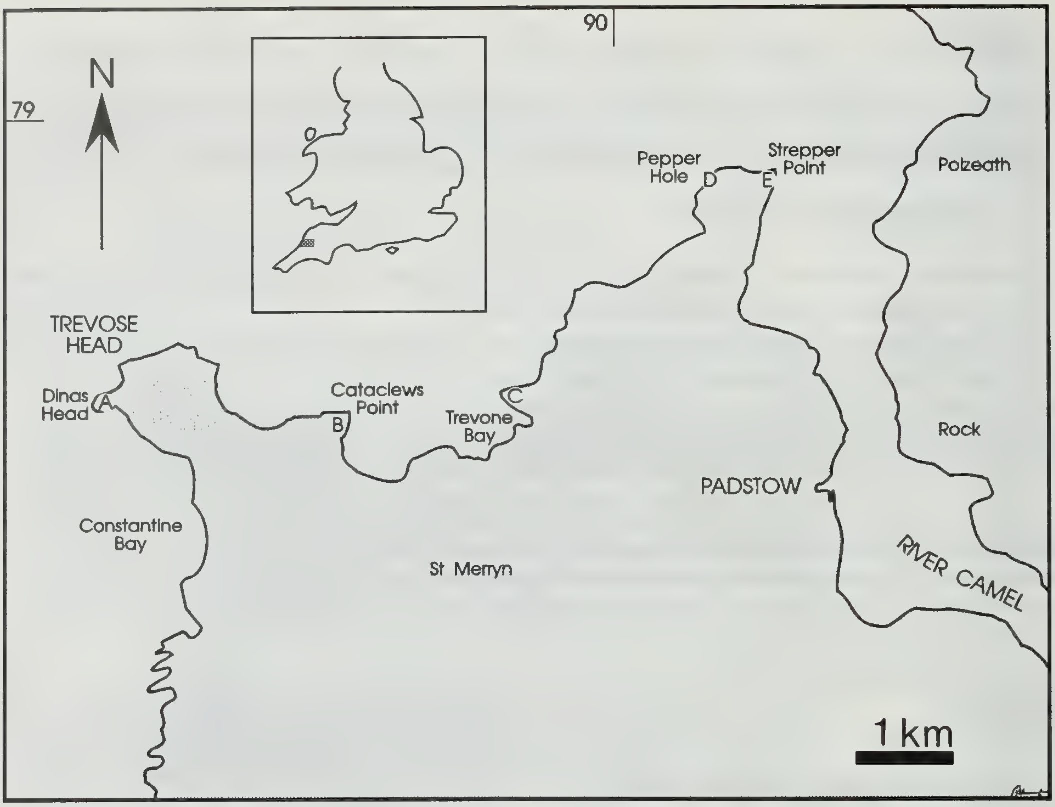

Fig. 1 Locality map of areas sampled. A = Dinas Head; B = Cataclews Point; C = Trevone Bay; D = Pepper Hole; E = Stepper Point.

and some keratophyric lavas and tuffs, and suggested that some rocks described as adinoles and of metasomatic origin are in reality tuffs altered by thermal metamorphism at the contact with basic intrusions. However, he concluded that the adinoles at Dinas Head were derived from a sediment, which had been metasomatised, and that the composition of the end-product adinoles is controlled by the metasomatic fluids emanating from the intrusive igneous dolerite rocks.

AIMS

From a systematic sampling of the adinoles, spilosites, slates and dolerites our aims were to: (1)Study the mobility and fixation of trace elements during the adinolisation process; (2)Investigate the formation of tourmaline (mobility and source of boron); (3)Compare the geochemistries of the dolerite and adinoles at Dinas Head with those of other similar rocks in the area; (4)Comment on the origin of adinoles.

In order to obtain representative samples for mineralogical and geochemical studies samples were collected from 3 measured sections of the Dinas Head rocks, the quarry section directly east of the headland and sites at Stepper Point, Pepper Hole, Trevone Bay and Cataclews Point (Figs 1 and 2). Details of the samples analysed are given in Table 1.

PETROLOGY AND MINERALOGY OF SAMPLES FROM DINAS HEAD

A comprehensive petrographic description of the rocks from Dinas Head was given by Agrell (1939), therefore the rocks studied here are only briefly described along with their mineral chemistries (below).

Dolerites

The massive intrusive units underlying the Dinas Head area and those studied from the Mackerel Cove, Stinking Cove and Quarry sections are albite-dolerites usually more than a metre thick with a mottled, dull dark-green surface. Below the High Water Mark (HWM), the dolerite has a weathered brown (limonitic) surface. At all localities it is extensively altered and little of the original mineralogy can be seen, but in less altered areas, ophitic textures can be recognised and some pyroxene is preserved. The areas of greatest alteration are marked by extensive chloritisation and carbonate development. The plagioclase feldspar (where unaltered) is albite (Ab_{90}) occurring as laths within the groundmass, and with pyroxene in ophitic texture. Light green chlorite with prussian blue interference colours, analyses in Table 2, often forms the matrix of the rock. An iron-rich carbonate occurs abundantly throughout the rocks, especially as small stringers. Ilmenite is common, mostly as skeletal plates and pyrite occurs in small amounts. Sample MC4 was collected close to

Table 1 Details of analysed samples.

Field No.	Lab. No.	Group No.	Details
MACKEREL COVE			
MC4	8466	2	Dolerite
MC5	8467	4	Sediment (carbonate-rich)
MC6	8468	4	Sediment (limestone)
MC7	8469	2	Dolerite
MC8	8470	4	Sediment (carbonate-rich)
MC9	8471	4	Sediment (carbonate-rich)
MC10	8574	1	Base of adinole (brown-spotted)
MC11	8575	1	0.3 m above MC10 (brown-spotted)
MC12	8472	1	6.0 m above MC10 (scarce brown spots)
MC13	8473	1	9.5 m above MC10 (green-spotted and banded)
MC15	8474	1	10.5 m above MC10 (massive adinole)
MC16	8475	1	17.0 m above MC10 (white massive adinole)
MC18	8476	1	24.0 m above MC10 (white, porcellaneous adinole)
MC21	8477	3	40.0 m above MC10 (white massive adinole)
MC22	8478	1	54.0 m above MC10 (white massive adinole)
MC23	8479	3	63.0 m above MC10 (white massive 'cherty' adinole)
STINKING COVE			
SC1a	8480	1	Spherulitic adinole
SC1b	8481	1	Spherulitic adinole
SC2	8482	4	Quartz-granite vein
SC3	8483	3	Adinole (2.0 m below SC1)
SC4	8571	4	Sediment (limestone)
SC5	8572	4	Sediment (carbonate-rich)
SC6	8484	1	Slate (fissile)
SC7	8573	4	Limestone band (2.0 m above faulted junction)
SC9	8485	2	Dolerite
SC10	8486	1	Adinole (1.0 m above adinole/dolerite contact)
SC11	8487	1	Adinole (20.0 m above adinole/dolerite contact)
SC14	8488	1	Adinole — brown-spotted (5.0 m above High Water Mark
SC15	8512	1	Adinole — brown-spotted (8.0 m above High Water Mark
SC16	8513	3	Adinole (due west of SC3)
SC17	8514	3	Adinole (directly below adinole/slate fault)
SC18	8489	3	Adinole (highest exposed outcrop)
SC19	8515	3	Adinole — green, massive (directly below adinole/slate fault
SC20a	8516	3	Adinole — green, massive (directly below adinole/slate fault
SC20b	8490	3	Adinole — black, massive (directly below adinole/slate fault
SC21	8517	3	Adinole (directly below adinole/slate fault)
47262	8502	3	From Agrell (1939), top of Stinking Cove
47263	8503	3	From Agrell (1939), top of Stinking Cove
47253	8504	3	From Agrell (1939), top of Stinking Cove
DINAS HEAD PROMONTORY			
DH1	8569	4	Dolerite?
DH4	8491	1	Adinole — brown, bedded (12.0 m above DH1)
DH5	8492	4	Adinole? — bedded (15.0 m above DH1)
DH6	8493	1	Adinole — grey, bedded (21.0 m above DH1)
DH7	8494	4	Shale — purple-grey with lozenges (26.0 m above DH1
DH9	8495	1	Adinole — white-weathered, massive (36.0 m above DH1
DH10	8570	2	Dolerite (47.0 m above DH1)
DH11	8518	1	Adinole (top of section, 56.0 m above DH1)
DINAS HEAD QUARRY			
DHQ3	8496	1	Adinole — grey-red, bedded
DHQ5	8566	1	Adinole — grey-red, slaty
DHQ6	8567	1	Adinole — brown-spotted
DHQ7	8497	1	Adinole — massive
DHQ8	8568	1	Adinole — white-weathered
DHQ9	8498	2	Dolerite — spotted
DHQ10	8499	1	Adinole
DHQ11	8500	4	Quartz vein
DHQ12	8501	2	Dolerite — altered
OTHERS			
PC5	8505	4	Sediment (Pepper Hole)
PC6	8506	2	Dolerite (Pepper Hole)
ST1	8673	4	Sediment (Stepper Point)
ST2	8674	2	Dolerite (Stepper Point)
ST5	8675	4	Slate (Stepper Point)
TR1	8676	2	Dolerite (Trevone Bay)
TR2	8677	4	Sediment (Trevone Bay)
TR3	8678	4	Slate — unaltered (Trevone Bay)
CAT2	8679	4	Sediment (Cataclews Point)
CAT3	8680	2	Dolerite (Cataclews Point)

Notes: Group 1 = sediments with Na_2O greater than 4.0%; Group 2 = dolerites; Group 3 = samples with boron greater than 400ppm; Group 4 = sediments with Na_2O less than 4.0%, and other samples

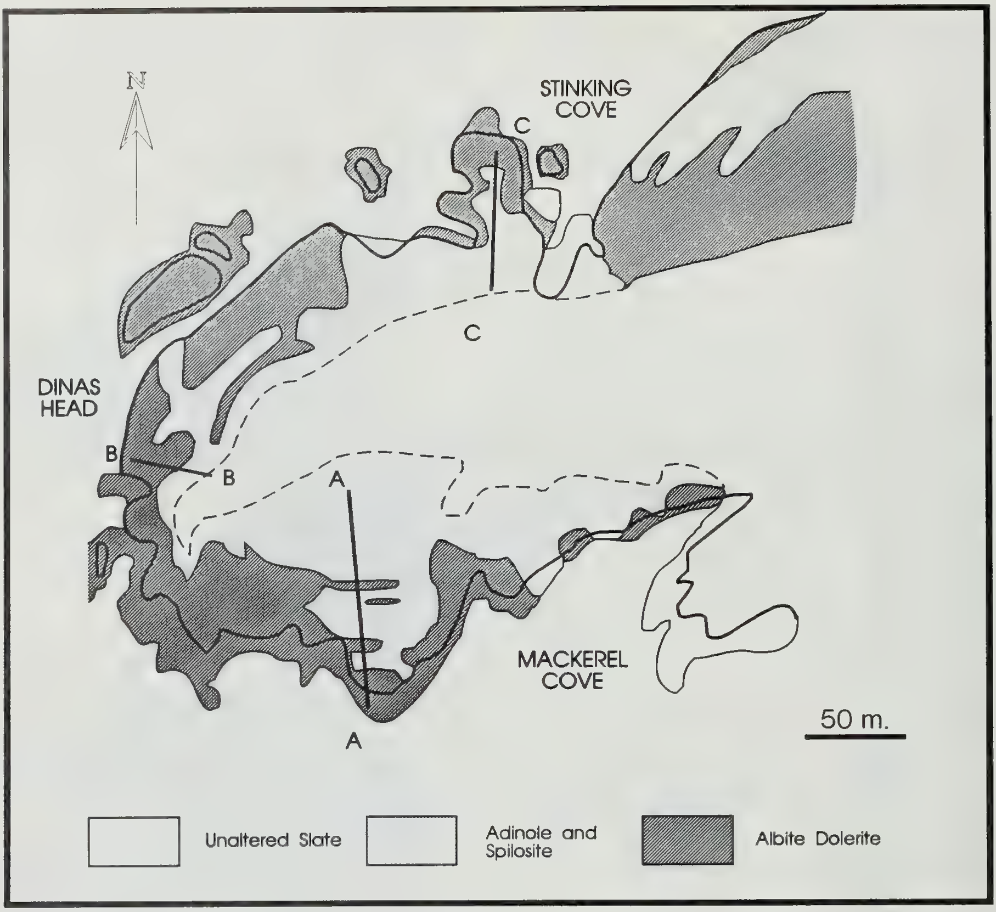

Fig. 2 Outline geological map (after Fox, 1895) of Dinas Head indicating locations of traverses A, B, and C for samples analysed.

the top of the dolerite intrusion at Mackerel Cove and consists of a mass of small euhedral albite crystals with chlorite, which may represent a chilled margin facies of the dolerite. The dolerite stringers (typically 25–50 cm thick) which cut the adinole sequence usually have been heavily carbonated and chloritised but original textures are better preserved with some remnant pyroxene. (Dolerite mineral analyses shown in Table 2, whole rock in Table 4).

Mackerel Cove section

The most complete sequence of adinole and spilosite development occurs above Mackerel Cove. A measured section was sampled from this area as shown in Fig. 2. Heights were recorded from the top of the massive dolerite intrusion found at HWM at intervals dependent upon change of rock lithology and texture.

The intrusive dolerite at the base of the section has an irregular surface from which smaller intrusions penetrate the sedimentary succession (Table 1). The beds of this sedimentary sequence dip between 20°–35° to the north and near the dolerite contact they are extensively quartz veined. The whole of this measured section was found to consist of various spilosite or adinole rocks. The distinctive white-weathering adinoles have a simple mineralogy of fine-grained albite and quartz, with minor chlorite, calcite and ankerite occasionally cut by thin carbonate-rich veins. Both calcite and ankerite are present as isolated, late-formed crystals or crystal patches. The carbonate-rich adinoles are often characterised by globular masses of ankerite up to 2 cm in diameter.

Above the extensive quartz veining is a somewhat irregular bed which is conglomeratic (or brecciated). Parts of this bed are extensively carbonated. Pebbles (?xenoliths) are albite-rich but much altered. This horizon is overlain by brown porcellaneous calcareous sediments, almost certainly originally limestone. These grade into a series of fine-grained, white and brown weathering rocks, containing extensive brown weathering (limonitic) iron oxides as spots and veins. Much of the iron oxide can be seen in thin section to be brown alteration products after pyrite. Above these beds, a major bluff is formed by rocks with distinct spotting and layering, these rocks have a very fine-grained matrix and are characterised by a random distribution of lozenge-shaped structures rimmed by iron carbonates. These beds are overlain by white-weathering rocks of a very fine grain size (albitic matrix) with dark diffuse spots of various sizes. None of the spots overprint original sulphide, most are diffuse pockets of albite and quartz with the original bedding often marked by black, filamentous material, probably graphite. Spots and veins rich in chlorite are also common in the rocks from this part of the section. Towards the top of the section spilosites comprising albite, quartz, chlorite, and filamentous carbon-

Table 2 Typical microprobe analyses of minerals from dolerites.

	MC2	MC2	MC4	MC4	MC7	MC7	DH2	DH10	DH10	DHQ9	DHQ9	ST2	ST2	TR1	TR1	TR1
	Albite	Chlorite	Albite	Chlorite	Albite	Chlorite	Albite	Albite	Chlorite	Albite	Chlorite	Albite	Chlorite	Albite	Clinopyroxene	Amphibole
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
SiO2	66.80	25.10	66.73	27.03	67.77	26.22	67.78	67.29	28.20	65.00	27.49	65.64	28.18	66.44	47.50	39.57
TiO2	<.05	<.05	<.05	<.05	<.05	0.09	<.05	<.05	2.78	<.05	0.09	0.00	<.05	<.05	2.04	4.89
Al2O3	20.20	20.48	20.09	19.12	19.26	20.05	19.61	19.86	17.31	21.56	17.99	20.59	16.54	20.26	5.46	11.94
FeO	0.53	28.81	0.26	29.59	0.19	25.08	0.80	1.09	21.83	0.40	26.57	0.56	25.94	0.30	6.28	13.66
MnO	<.05	0.11	<.05	0.11	<.05	0.20	<.05	<.05	0.06	<.05	0.07	<.05	0.07	<.05	0.17	0.18
MgO	<.05	10.59	<.05	10.70	<.05	13.21	<.05	<.05	15.81	<.05	13.50	<.05	15.39	<.05	13.14	10.80
CaO	0.61	0.13	0.51	0.21	0.13	0.09	0.14	0.15	0.00	1.82	0.17	0.82	0.19	0.25	22.83	11.67
K2O	0.22	0.15	0.24	0.08	0.03	0.10	0.72	0.03	0.19	0.14	0.08	0.47	0.15	0.54	<.02	0.99
Na2O	11.60	0.22	11.29	0.64	11.99	0.49	10.37	11.63	0.17	10.92	0.34	10.41	0.38	10.47	0.55	2.96
TOTAL	99.96	85.59	99.12	87.48	99.37	85.53	99.42	100.05	86.35	99.84	86.30	98.49	86.84	98.26	97.97	96.66
Ab	96.0		96.3		99.2		95.0	99.1		90.8		93.2		95.5		
An	2.8		2.4		0.6		0.7	0.7		8.3		4.1		1.3		
Or	1.2		1.3		0.2		4.3	0.2		0.9		2.7		3.2		

Analyses 1–6. Mackerel Cove section.
Analyses 7–9. Dinas Head section
Analyses 10–11. Dinas Head Quarry section.
Analyses 12–13. Stepper Point
Analyses 14–16. Trevone Bay.
Analyses made by energy-dispersive microprobe.

aceous material predominate. There are also calcite-rich spots, with the calcite present either as single crystals or as clusters. At the top of the section, the rocks are a mixture of spilosites and adinoles, with coarse- to fine-grained albite, aggregates of leucoxene (after anatase) and quartz veining. Microprobe analyses of albite and chlorite from several samples are given in Table 3. Chemical analyses of two samples, MC21 and MC23 (Table 4), showed them to be boron-rich.

Stinking Cove section

The Stinking Cove section (Fig. 2) is extensively faulted and a complete succession cannot be traced. However, the section is of importance in that it contains excellent examples of polygonal (spherulitic) adinole development, and areas of high boron content, as ascertained by chemical analysis.

On a rock shelf above the dolerite contact and above the HWM is a spectacular development of spherulitic and polygonal adinole, not seen elsewhere on Dinas Head. These rocks grade above and below into apparently normal adinoles. However, chemical analyses and scanning electron microscopy indicate that some of these rocks are K-rich, and that white mica (probably sericite, e.g. Fig. 3b) predominates over albite. Much of this area is ribbed by thin veins of carbonate and the faulted western margin is marked by coarse quartz veining carrying lead mineralisation (SC2, Table 4). To the south, the adinoles are cut out by a fault and the resultant low cliff section comprises unaltered slates and massive limestone bands. These rocks do not show evidence of adinolisation or spilositisation. The rocks above and below the polygonal development show, on analysis, the patchy development of high boron-rich areas (e.g. SEM photo, Figs 3c, 3d), which is consistent with Agrell's (1939) report of colourless dravite in the rocks, although the matrix is often sericite-rich, not albite-rich.

In this section, the rocks are typically composed of a fine-grained groundmass of albite, and/or sericite, containing small spots with opaque centres. Some of the spots are carbonate and/or chlorite-rich. Small skeletal ilmenite grains are common and in places appear to pick out original bedding in the rocks. At x100 magnification the groundmass of the boron-rich rocks is indistinguishable from that of boron-poor rocks, except that they consist almost entirely of a mat of small albite laths and show very little spot development or carbonatisation (e.g. SEM photo, Fig. 3a).

The polygonal adinole consists of a fine-grained skeletal framework forming irregular 5–10 mm sided polygons, the whole structure consisting of a groundmass of albite, quartz and chlorite. Original bedding can be recognised and Agrell (1939) has proposed that these adinoles be divided into different types because the albite in some parts is coarser and forms a (crude) spherulitic texture. The edges of both the polygonal and spherulitic types tend to stand out as weathered surfaces. Ankerite occurs both as ribs between some of the polygons, and as individual rhombs. Small black filamentous (carbonaceous) stringers were seen in some of the thin sections studied and thin quartz veins cut all types of structure.

Closer to the dolerite contact, within an unfaulted part of the sequence, a series of spotted rocks similar to those described from elsewhere on Dinas Head and Stepper Point is exposed. These spotted rocks contain larger, often diffuse carbonate-rich spots or structures, which often appear to be aligned along bedding. The groundmass consists of fine-grained albite and chlorite, and small skeletal ilmenite grains and sulphide blebs. The centres of the larger carbonate-rich spots are often cavernous and many have a rim accentuated by colouration due to brown limonite after ankerite.

Within a faulted block of this rock succession, closest to the contact with the massive dolerites, spilosites are abundantly developed. These rocks, with a matrix of albite and feather-

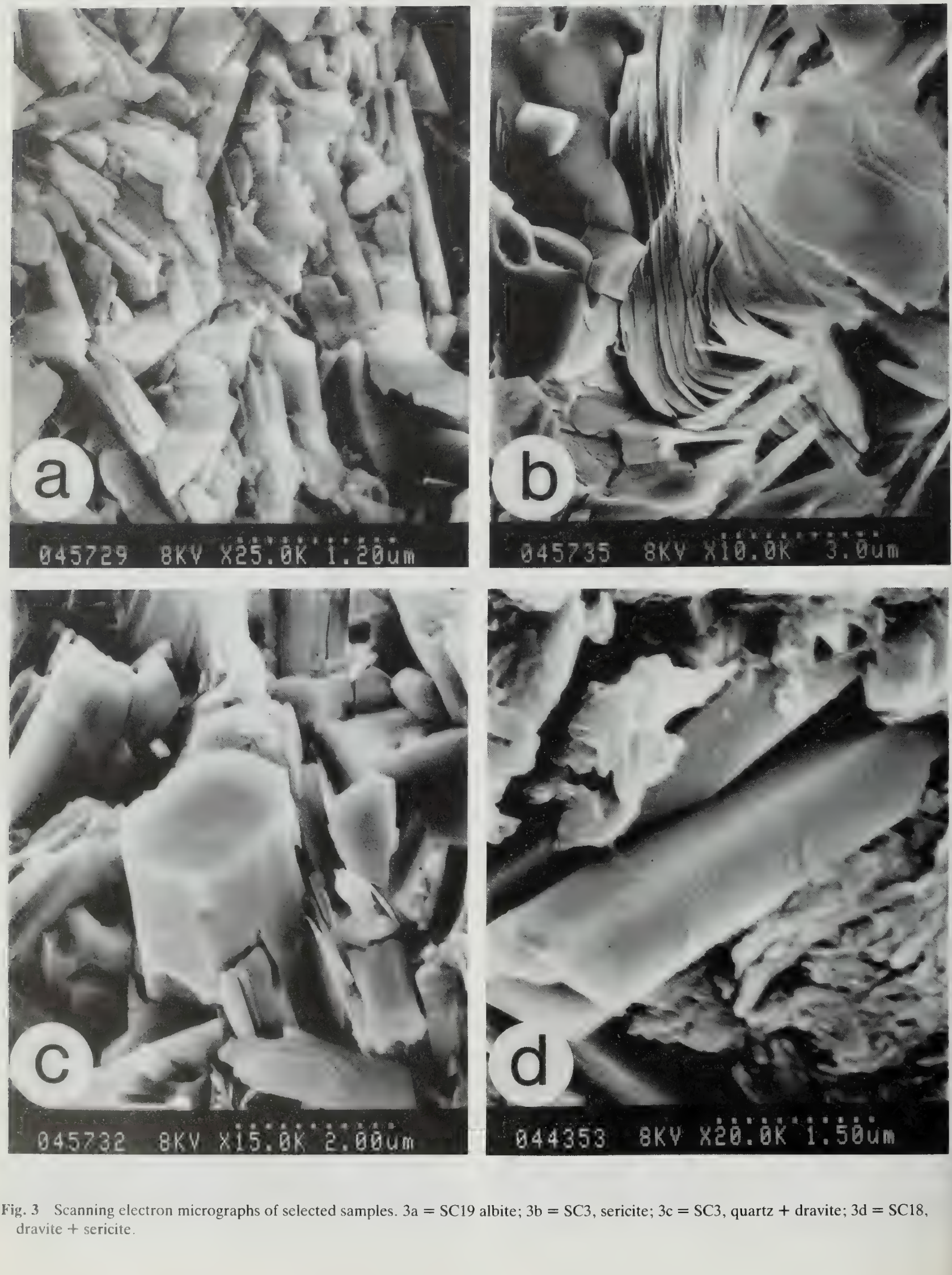
a
045729 8KV X25.0K 1.20um
b
045735 8KV X10.0K 3.0um
c
045732 8KV X15.0K 2.00um
d
044353 8KV X20.0K 1.50um

Fig. 3 Scanning electron micrographs of selected samples. 3a = SC19 albite; 3b = SC3, sericite; 3c = SC3, quartz + dravite; 3d = SC18, dravite + sericite.

ing stringers of chlorite, are rather different from the typical rocks seen in other sections.

Dinas Head section

The measured section at the western extremity of Dinas Head (Fig. 2) is a succession of spilosites and adinoles interdigitating with thin dolerite intrusions above massive weathered dolerite. The top of the massive dolerites is extensively sheared and veined with quartz.

Like the sections at Stinking Cove and Mackerel Cove, the sequence at Dinas Head is a series of spilosites and adinoles with different textures. Predominant is a grey weathering, fine-grained bedded sequence with brown ankeritic rich spots. Another common feature of the rocks in this section is the prevalence of patches of chloritic alteration. Recognisable in hand specimen, these patches show no definable or constant shape, and often consist of a central core of calcite rhombs enclosing ilmenite grains. Altered sulphide grains (mostly pyrite) impart brown spotting to weathered surfaces. These rocks grade into fine-grained albite-rich rocks, which display remnants of the original bedding (emphasised by carbonaceous filaments). They are also characterised by small calcite patches, spots and frequent limonite-lined calcite veining.

Some 25 m above the top of the dolerite there is a good example of the limonite-rich, 'lozenge' textured rocks, similar to those described from the Stepper Point locality. These rocks have a fine-grained albitic matrix, with carbonaceous filaments and substantial thin veining, most of which is chlorite-rich. Here the lozenge structures, essentially comprising calcite and lined with brown iron oxides, must be formed late because they cut both the chlorite veins and carbonaceous filaments. These rocks grade into massive bedded units of spilositic texture. The top of this section is marked by banded, white-weathering adinoles with a matrix of albite and chlorite. Sericite-rich rocks were not observed here.

Quarry section

The section exposed in the quarry at the eastern end of the Dinas Head promontory has been extensively folded and faulted, such that the relationships between individual parts cannot be traced. The section consists of a repeatedly sheared sequence of black and purple slates (shales). Although the section is intruded by massive dolerite units to the south, most of the shales do not appear to have been altered and are similar to the beds at the top of the Stinking Cove section. However, toward the centre of the section, between two convergent shear zones, some spotted rocks have been developed. These rocks have a fine-grained albitic matrix. The spots are dark, intense in appearance, and often preferentially aligned. Lozenge shaped structures, such as those found at Dinas Head, also occur.

The dolerite in the quarry section is medium-grained but very altered, and in places has a 'spotted' surface appearance.

OTHER AREAS OF STUDY

The succession of rocks from Dinas Head, described as adinoles, is very much thicker (approximately 60 m) than other recorded adinole sequences, especially in comparison with potentially similar rocks directly associated with intrusive dolerite complexes in the same province of Cornwall. Dolerites are exposed along the coastal sections from Dinas Head eastwards to Stepper Point, where the associated sediments close to the contacts with the dolerite are often characteristically fine-grained, white-weathering with carbonate 'spot' and vein growth (cf. Dinas Head — Stepper Point occurrences). Samples of both dolerite and contact country rock have been sampled and analysed for comparison with those at Dinas Head (Tables 1 and 4). A brief field and petrological description of these rocks is given below.

Table 3 Typical microprobe analyses of minerals from adinoles and spilosites.

	MC10 Albite	MC12 Albite	MC13 Albite	MC13 Chlorite	MC14 Albite	MC14 Chlorite	MC15 Albite	MC15 Chlorite	MC23 Albite	MC24 Albite	SC1 Albite	SC10 Albite	SC14 Albite	ST1	TR2	PC5
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
SiO2	67.86	68.88	66.65	25.51	67.29	24.79	67.79	26.14	67.69	67.82	67.19	68.46	67.1	58.45	55.32	64.67
TiO2	0.07	0.08	<.05	<.05	<.05	0.05	<.05	<.05	0.12	<.05	<.05	0.07	0.15	<.05	0.43	<.05
Al2O3	19.08	19.01	19.34	21.65	18.83	21.2	18.84	21.04	19.11	19.12	19.7	18.89	19.06	22.00	24.14	19.23
FeO	<.05	<.05	0.12	28.61	1.25	28.8	0.22	29.81	0.14	0.4	0.15	0.11	0.1	2.37	1.43	5.72
MnO	0.11	<.05	<.05	<.05	<.05	0.17	<.05	0.13	<.05	<.05	<.05	<.05	<.05	<.05	0.15	<.05
MgO	<.05	<.05	<.05	9.41	0.13	9.27	<.05	7.78	<.05	<.05	<.05	<.05	<.05	1.34	1.09	2.78
CaO	0.15	0.06	0.21	0.17	0.05	0.05	0.12	0.17	0.04	0.08	0.1	0.1	0.15	0.27	0.1	<.05
K2O	0.11	0.08	0.03	0.12	0.09	0.12	0.01	0.1	0.11	0.22	0.34	0.24	0.04	6.84	7.3	4.14
Na2O	10.90	10.67	11.28	0.37	10.47	0.18	10.83	0.52	10.99	10.69	11.1	10.14	11.02	0.09	0.18	<.05
TOTAL	98.28	98.78	97.63	85.84	98.11	84.63	97.81	85.69	98.2	98.33	98.58	98.01	97.62	91.36	90.14	96.54
Ab	98.6	99.2	98.8		99.2		99.3		99.2	98.3	97.5	98.0	99.0			
An	0.8	0.3	1.0		0.2		0.6		0.2	0.4	0.5	0.5	0.7			
Or	0.6	0.5	0.2		0.6		0.1		0.6	1.3	2.0	1.5	0.3			

Analyses 1–10. Mackerel Cove section, adinole and spilosite.
Analyses 11–13. Stinking Cove section
Analysis 14. Stepper Point
Analysis 15. Trevone Bay
Analysis 16. Pepper Hole

Stepper Point (GR SW 916,785)

The best exposures of the dolerite-sediment contacts outside the Dinas Head area are at Stepper Point. Here, thick dolerite intrusions have been extensively quarried and relatively fresh sections can be sampled. Within the southern section of these quarries the contact between the dolerite and the country rocks is well exposed. Although the country rocks vary from grey to green to purple slates, the rocks adjacent to the contact are spotted spilosites, with small, dark grey, diffuse spots. The more diffuse spots often contain minute black areas, which are not sulphide or limonite-rich and may be original carbonaceous material. A characteristic feature of these rocks is that within a metre of the contact, ferruginous, calcareous nodules are developed, the cores of which are often weathered out and slightly elongated along bedding. Further from the contact, the country rock sequence of grey/green/purple slates prevails.

Specimens of dolerite were sampled from the centre of the intrusion in the main quarry and also from close to the contact. Although the hand specimens appeared relatively fresh, thin section examination revealed all samples as being extensively altered. Electron microprobe analyses and whole rock chemical analyses are shown in Tables 2 and 4. In hand specimen the dolerites are a dull, grey-green colour and essentially non-porphyritic. Thin sections show characteristic clots of intergrown feldspars (albite Ab_{93} — see Table 2), which are occasionally clear, but usually sericitised. The pyroxene, originally augite, has been extensively altered to chlorite and a dark brown product of variable compositions; ophitic textures can still be recognised. Large ilmenite masses and copious euhedral apatites are common in all the thin sections studied.

Thin section examination of those rocks directly above the contact, showed that they are spilositic in texture, very fine grained and often have a calcareous matrix. The rock is distinctly spotted, often with minute dark spots which appear to be formed from remnant organic material. Within 25 cm of the contact, these fine-grained spilosites merge into similar fine-grained rocks with distinct lozenge-shaped ferruginous, calcareous structures. The matrix of these rocks is consistently of a sericitic composition.

Pepper Hole (GR SW 907,782)

Samples of dolerite and associated purplish-grey slates were collected from a cliff section above the main dolerite intrusion. Here the dolerites occur as thin sills, up to 10 cm thick, being stringers from the massive dolerite intrusion cutting through the succession of purple-red-grey slates. The argillaceous rocks consist of a matrix of very fine-grained sericite incorporating about 10% quartz and feldspar fragments. The rocks are cut by minor limonite-stained calcite veins. No preferred orientation was observed to the fabric of these rocks, and, although they do contain many altered limonitic blebs, they do not have the typical spilositic (or adinole) texture or composition. This indicates a very low level of alteration by the associated minor dolerite intrusions. The medium-grained dolerite is considerably altered — pyroxene to chlorite and feldspar to sericite — but remnant ophitic texture is present. Apatite and ilmenite are common in the groundmass.

Trevone Bay (GR SW 889,764)

To the north of Trevone Bay and immediately west of the eroded 'blow-hole' shown on the O.S. map as Round Hole, a massive dolerite intrusion cuts through sediments comprising alternating bands of slates and limestones.

The non-porphyritic dolerite has mostly a weathered limonitic surface and is in contact with a series of mainly bleached, poorly spotted slates (spilosites). These are extensively veined by both quartz and calcite. Although in hand specimens the dolerite appears extensively weathered, thin section examination shows it is less altered than dolerites from other localities sampled in this study. However, it does contain considerable interstitial calcite. The dolerite is rich in augitic pyroxene, brown hornblende, chlorite and laths of albitic plagioclase feldspar. Although pyroxenes are often altered to amphibole there is only minor alteration of the amphibole to chlorite. Apatite and ilmenite are common as euhedral crystals, and calcite occurs interstitially. Typical analyses of the major phases are shown in Table 2.

The dolerite intrusion appears to have altered the surrounding sediments to typical spilosites, characterised by small dark grey-black spots, these sometimes associated with small pyrite crystals which are often altered to limonitic pseudomorphs. The fine grained matrix and diffuse spots are sericitic in composition (Table 3). Whole rock analyses of dolerite and spilosite are given in Table 4.

Cataclews Point (GR SW 873,762)

At Cataclews Point massive dolerite sills cut a succession of slates, some interbedded limestones and cherts. The shales (slates) in close contact with, or engulfed by the dolerites are bleached and have a typical spilositic texture. This section has been extensively sheared and parts of the sequence have been described as cataclasites (Fox, 1895). Samples were collected from the less tectonised areas where igneous-sedimentary contacts could be recognised. Even so the coarse-grained dolerites in thin sections were found to be extensively altered with almost complete sericitisation of the feldspars and chloritisation of mafic phases. Where clear (unaltered) feldspar laths were analysed, the composition is varied, but not albitic. Very little original pyroxene remained, but textures suggest replacement by both green and brown amphibole, the latter being a Ti-rich variety. Pyrite and ilmenite are both present in the rock.

The associated sedimentary rocks have a very fine grained sericitic matrix and conspicuous spotting, often with a slight elongation of the spots. These rocks have abundant, small spots of a similar size; spots and matrix are generally of a similar sericitic composition although the spots are relatively iron rich. Whole rock analyses are given in Table 4.

ANALYTICAL METHODS

The specimens collected were crushed in a jaw crusher and comminuted to a particle size of $\ngtr 180\mu m$ by grinding in agate. All powders were dried at 110°C prior to sampling for analysis. Deionised water and analytical grade reagents (or better) were used throughout the various preparation procedures.

Major and minor elements

Approximately 100 mg of powder, accurately weighed, was mixed with 500±1 mg of lithium metaborate flux in a platinum/5% gold crucible and fused at 950°C until a transparent melt was obtained. The hot fusion bead was quenched in 140 ml of dilute nitric acid (1M), contained in a plastic beaker, and the mixture was stirred at ambient temperature until the solid dissolved. The clear solution was washed into a 250 ml volumetric flask and made to volume with water.

Analyses of the prepared solutions for Si, Ti, Al, total Fe, Mn, Mg, Ca, Na and K were made by inductively-coupled plasma (ICP) emission spectrometry using a Fison's ARL 3410 Minitorch machine. The instrument parameters were adjusted according to the manufacturer's recommendations and the system was calibrated with a series of multi-element synthetic standards prepared from commercial, spectroscopically pure, stock solutions. Appropriate corrections were made to compensate for background emission and instrumental drift. Several international standard reference rocks were processed as unknown samples in order to verify the accuracy of the procedure.

Combined water and total carbon, expressed as CO_2 were determined in accurately weighed sample aliquots of approximately 25 mg following the procedure described by Din and Jones (1978). Ferrous iron was estimated volumetrically by titration with standardised potassium permanganate, a variation of the method described by French and Adams (1972).

Trace elements

Up to 27 trace elements were determined by instrumental neutron activation analysis (INAA) and ICP. Not all of the elements listed below were determined in all samples.

Solutions for the determination by ICP of Ba, Be, Cu, Li, Nb, Ni, Pb, Sr, V, Y, Zn and Zr were prepared using a standard perchloric-hydrofluoric acid procedure to dissolve 1 g of rock in a final solution volume of 50 ml.

INAA data for selected rare earth elements (REE), As, Cr, Co, Cs, Hf, Rb, Sb, Sc, Ta, Th and U were obtained from 100 mg of rock powder following the technique described by Williams and Wall (1991).

Boron

Boron was measured quantitatively by ICP in the aqueous leachates (25 ml) prepared from a fused mixture of sodium carbonate (500±1 mg) and about 50 mg of accurately weighed sample powder. Sulphur and phosphorus were measured in the same solutions.

Qualitative maps of the boron distribution in thin sections of selected samples were made, using the solid state nuclear track detection technique, according to the procedure described by Din and Henderson (1982).

Data for boron isotope studies were obtained by ICP mass spectrometry, using equipment at the British Geological Survey Laboratories, Gray's Inn Road, London WC1. Solutions of the samples, together with a National Bureau of Standards isotopic reference (SRM951), were prepared from the powdered materials after fusing with 1000±30 mg of potassium hydroxide in vitreous carbon crucibles and leaching and dissolving in 50 ml dilute nitric acid (1M). These solutions were made up to 200 ml and tenfold dilutions were prepared for ICPMS. Sample weights were chosen to yield solutions containing <5 ppm boron on dilution.

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Dolerites

At Dinas Head, dolerite is seen in three localities — at Mackerel Cove and Stinking Cove, where it forms the base of the promontory (Fig. 1), and in the quarry section to the east. At Mackerel Cove, and to a lesser extent at Stinking Cove, the dolerite often occurs interfingered with the associated adinoles although actual contacts were not observed. In the field, the dolerite appears evenly medium-grained and relatively fresh at the promontory, but is more altered in the quarry section, and in places has a 'spotty' appearance.

Six samples of the dolerite were selected for chemical analysis — two from the Mackerel Cove section, one from Stinking Cove, one from Dinas Head and two from the quarry section. The results (Table 4), show many similarities for all samples, and particularly for those elements considered to be less mobile during alteration processes, i.e. the REE, Hf, Ta and Th, indicating that the dolerite is likely to be a single intrusion. The overall chemical composition of the dolerite is similar to that of other Upper Palaeozoic tholeiitic basalts from south-western England (Floyd 1982).

Dolerites from four other localities in N. Cornwall, reported to be associated with adinoles, were also sampled and analysed. These were from Pepper Hole, Stepper Point, Trevone Bay and Cataclews Point: data are given in Table 4. From a comparison of these data with those from Dinas Head, Table 4, and associated diagrams (Fig. 4), it is clear that for many elements significant differences exist between the dolerite from Dinas Head and those from Pepper Hole and Trevose Head, and minor differences between Dinas Head dolerites and those from Stepper Point. There is however a strong similarity between the dolerites from Dinas Head and those from Cataclews Point; compare for example data for elements Sc, Co, Ta, Th, U and REE, Table 4.

Sediments

A total of 54 sediments were selected for whole rock geochemistry, 49 of those from the four sampled sections of the Dinas Head area. The remaining sediments analysed were those associated with the dolerites from Stepper Point, Pepper Hole, Trevone Bay and Cataclews Point.

Sediments from the Dinas Head sections are plotted on the $(Na_2O.Al_2O_3) - (K_2O.Al_2O_3) - (Fe_2O_3 + FeO + MgO + MnO + CaO)$ ternary diagram (Fig. 5) following Agrell (1939), in order to ascertain which sediments plot in the 'adinole', 'spilosite + desmosite' and 'slate' fields. There is a relatively good correlation with Na_2O% and little overlap within the discriminated fields. Those plotting in the 'adinole' field have Na_2O contents ranging from 6.22% (MC10) to 11.10% (SC11), those in the 'spilosite + desmosite' field range from 1.64% (47263) to 7.35% (MC13) and those in the 'slate' field have Na_2O contents <1.64%.

From this diagram also, it can be seen there is a complete gradation from Na_2O-rich, K_2O-poor sediments (e.g. MC11, $Na_2O = 9.86\%$; $K_2O = 0.20\%$) in the 'adinole' field, to Na_2O-poor, K_2O-rich sediments (e.g. SC20A, $Na_2O = 0.51\%$; $K_2O = 4.56\%$) in the 'slate' field. In the 'adinole'

Table 4 Chemical analyses of whole rock samples.

SAMPLE	MC4	MC5	MC6	MC7	MC8	MC9	MC10	MC11	MC12	MC13	MC15	MC16	MC18	MC21	MC22	MC23	SC1A
SiO_2	46.3	50.2	9.50	50.8	47.5	47.6	70.9	68.7	63.5	55.8	57.2	69.4	66.6	70.3	71.0	66.1	63.0
TiO_2	1.71	0.41	0.01	1.61	1.30	1.16	0.61	0.65	0.61	0.82	0.69	0.50	0.68	0.69	0.58	0.68	0.55
Al_2O_3	15.8	8.10	1.37	16.3	15.6	14.9	12.8	16.7	16.6	20.0	19.1	13.6	18.6	17.2	16.7	19.8	17.2
Fe_2O_3	1.23	0.03	0.82	1.29	0.56	0.37	1.89	0.67	0.80	2.39	1.06	0.88	0.14	0.42	0.05	0.00	0.20
FeO	8.43	5.43	11.1	8.56	7.02	6.40	0.15	0.10	1.17	5.88	7.89	4.06	0.79	0.34	0.45	0.51	0.61
MnO	0.12	0.21	0.34	0.09	0.11	0.09	0.08	0.03	0.06	0.03	0.03	0.05	0.03	0.02	0.02	0.02	0.06
MgO	4.09	4.29	8.72	5.46	5.76	6.95	0.28	0.05	1.28	2.48	2.30	1.70	0.53	0.62	0.36	1.05	0.72
CaO	6.25	11.2	27.3	2.91	5.39	5.39	2.75	0.38	3.28	0.20	0.16	1.20	0.70	0.09	0.08	0.15	3.91
Na_2O	4.38	1.11	0.14	4.70	2.35	2.53	6.22	9.86	8.15	7.35	7.03	5.43	10.40	8.60	9.17	8.35	8.58
K_2O	0.83	1.46	0.21	0.47	1.90	1.52	0.67	0.20	0.22	0.43	0.26	0.15	0.18	0.10	0.08	0.25	0.30
P_2O_5	0.19	0.09	0.03	0.09	0.15	0.11	0.20	0.26	0.09	0.20	0.16	0.07	0.09	0.05	0.08	0.14	0.03
H_2O^+	3.84	1.43	0.48	4.08	4.01	4.23	1.02	0.32	0.87	3.03	3.14	2.06	0.58	0.51	0.44	0.68	0.69
CO_2	5.35	16.2	37.9	3.66	7.54	7.59	2.65	0.31	3.51	0.15	0.07	1.10	0.60	0.22	0.13	0.20	3.01
others	0.43	0.27	0.14	0.41	0.26	0.29	0.14	0.07	0.12	0.98	0.32	0.22	0.12	0.91	0.12	1.44	0.21
O=S	–0.09	–0.05	–0.00	–0.10	–0.01	–0.01	–0.01	0.00	–0.00	–0.38	–0.07	–0.05	–0.00	–0.01	–0.01	–0.01	–0.01
TOTAL	98.9	100.3	98.0	100.3	99.4	99.1	100.3	98.3	100.3	99.4	99.3	100.4	100.0	100.1	99.2	99.4	99.1
$Fe_2O_3(T)$	10.6	6.06	13.1	10.8	8.36	7.48	2.06	0.78	2.10	8.92	9.83	5.39	1.02	0.80	0.55	0.44	0.88
S	1900	1100	80	2000	200	200	200	<50	90	7600	1500	1000	50	200	200	300	200
Be	1.7	1.4	0.8	1.3	1.8	2.1	0.8	0.6	1.1	1.4	1.6	1.0	0.9	0.9	0.7	1.9	1.0
Li	123	38	9	129	118	155	27	5	27	141	131	88	17	7	13	2	14
B	<25	40	<25	<25	40	40	25	<25	<25	<25	<25	<25	<25	2500	<25	4100	80
Sc	34.2	13.5	9.1	32.2	26.2	26.6	15.2	9.7	13.9	18.2	18.0	8.5	15.2	17.9	10.4	14.7	12.3
V	245	125	66	234	191	199	110	54	83	180	158	83	119	97	90	123	102
Cr	222	85	12	324	243	339	104	72	85	117	103	77	90	104	82	116	148
Co	33.0	12.0	6.3	40.0	32.3	29.6	2.6	0.5	5.0	37.7	23.9	23.6	13.8	2.7	1.5	0.9	1.5
Ni	20	43	21	64	105	171	25	10	40	102	163	82	117	29	71	nf	63
Cu	31	19	23	17	19	20	8	5	22	40	20	37	6	5	5	8	34
Zn	57	24	21	49	63	42	61	10	44	44	26	34	19	9	8	20	307
As	20	19	1	24	42	50	24	6	6	63	19	28	1	7	3	2	nf
Rb	47	81	21	20	140	83	33	5	60	60	65	65	40	50	50	50	30
Sr	603	352	726	201	232	340	160	147	155	126	92	88	122	89	116	98	228
Y	22	21	31	18	20	17	19	17	16	20	14	12	10	5	24	10	34
Zr	88	47	22	72	110	75	102	107	95	130	120	92	108	100	80	100	100
Nb	11	7	9	11	10	12	9	11	10	9	8	7	15	15	11	1	16
Sb	6.4	2.6	0.6	2.8	3.4	4.5	6.2	3.8	1.9	1.6	nf	1.8	1.0	1.6	0.7	1.1	1.3
Cs	7.0	5.3	1.7	2.1	7.9	8.8	2.3	0.7	1.1	1.2	1.2	0.8	0.6	0.5	0.7	0.7	0.9
Ba	112	95	16	60	118	129	66	23	27	37	28	15	23	17	18	30	30
La	7.5	15.9	5.1	13.3	17.8	27.2	11.4	14.0	21.4	95.0	33.5	21.6	38.8	9.5	20.7	3.3	5.8
Ce	17.9	26.6	13.0	29.5	30.3	45.8	21.0	22.5	58.3	180.0	59.8	47.1	65.8	21.5	62.0	5.8	15.5
Nd	12.8	13.8	11.5	15.7	16.7	22.4	11.0	9.5	33.8	80.2	21.2	26.4	22.2	8.3	39.8	4.6	8.4
Sm	3.28	3.38	4.12	3.47	3.94	3.92	2.28	2.18	6.38	12.20	4.79	4.52	3.64	1.67	5.46	1.45	2.19
Eu	1.59	1.36	2.86	1.02	1.10	0.85	0.63	0.46	0.98	2.36	0.99	0.95	0.55	0.33	0.48	0.23	0.52
Gd	4.6	2.7	5.2	3.3	3.9	2.8	2.9	3.3	5.3	10.5	5.4	3.6	2.8	1.5	5.5	1.5	4.3
Tb	0.71	0.57	0.89	nf	0.76	0.60	0.45	0.35	0.67	1.78	0.71	0.50	0.40	0.18	0.96	0.25	0.74
Tm	0.27	0.26	0.41	0.32	0.45	0.36	0.24	0.22	nf	0.85	0.39	0.30	0.27	0.11	0.52	0.00	0.66
Yb	2.10	1.41	1.64	1.85	2.24	1.80	2.05	1.90	1.89	5.65	2.22	1.82	1.15	0.66	2.91	1.38	3.23
Lu	0.27	0.21	0.21	0.26	0.32	0.24	0.29	0.28	0.23	0.74	0.22	0.24	0.16	0.12	0.36	0.19	0.47
Hf	2.2	0.9	0.2	2.3	2.8	2.0	2.5	2.7	2.7	4.0	3.4	2.0	3.2	3.1	2.7	3.2	3.0
Ta	0.48	0.22	0.05	0.51	0.49	0.35	0.81	0.92	0.80	1.23	1.00	0.67	0.98	0.94	0.87	1.00	0.92
Th	0.65	1.90	0.20	0.70	0.83	1.20	7.00	8.40	8.30	18.60	9.20	7.30	7.30	8.00	8.60	10.00	10.10
U	0.2	0.5	0.2	0.3	0.7	0.9	2.4	1.4	1.2	2.9	2.2	1.5	1.6	1.8	2.1	2.5	2.4
Pb	24	28	51	48	38	50	16.7	19.8	7	20	14	17	15	13	8	27	47

Table 4 *contd.*

SAMPLE	SC1B	SC2	SC3	SC4	SC5	SC6	SC7	SC9	SC10	SC11	SC14	SC15	SC16	SC17	SC18	SC19	SC20A
SiO_2	58.8	87.1	47.8	4.09	30.5	59.4	0.34	41.4	60.7	63.4		65.0	66.5	47.0	38.0	76.7	68.3
TiO_2	0.50	0.09	1.25	0.03	0.03	0.87	nf	1.33	0.70	0.75		0.61	0.66	1.41	1.37	0.50	0.89
Al_2O_3	16.3	1.32	28.4	0.41	0.71	21.9	0.02	14.4	17.9	18.5		17.2	18.8	32.7	35.8	13.9	21.7
Fe_2O_3	0.43	0.22	0.00	1.22	11.90	1.81	0.08	1.00	0.30	0.07		0.16	0.13	0.23	0.62	0.20	0.31
FeO	1.19	1.88	1.81	0.58	0.24	3.81	0.47	8.71	0.47	0.20		0.43	0.10	0.14	0.71	0.32	0.08
MnO	0.10	0.03	0.03	0.36	0.55	0.04	0.14	0.16	0.07	0.05		0.02	0.01	0.01	0.02	0.01	0.01
MgO	1.28	0.60	6.00	0.22	0.60	1.77	0.32	8.11	1.10	0.40		1.64	0.69	2.38	6.54	1.91	0.58
CaO	6.07	0.01	1.47	53.3	28.4	0.03	55.7	7.18	4.65	2.20		2.49	0.85	0.33	0.54	0.45	0.08
Na_2O	7.67	0.23	1.50	0.10	0.17	0.59	0.03	1.55	8.63	11.10		6.81	8.56	0.86	1.57	0.43	0.51
K_2O	0.42	0.24	0.92	0.23	0.34	3.78	0.18	1.59	1.12	0.74		1.14	0.83	4.60	1.02	1.11	4.56
P_2O_5	0.02	0.08	0.12	0.02	nf	0.17	nf	0.11	0.14	0.15		0.31	0.04	0.22	0.29	0.01	0.05
H_2O^+	1.24	1.00	2.71	0.48	2.73	4.83	0.28	5.28	1.29	0.64		0.94	0.63	6.08	3.62	1.75	3.36
CO_2	4.92	0.69	1.15	39.8	22.2	1.59	42.6	8.13	2.90	2.02		2.86	0.63	0.14	0.26	0.60	0.18
others	0.26	6.84	7.70	0.06	0.12	0.31	0.09	0.33	0.15	0.14	0.06	0.15	0.25	2.42	8.55	2.77	0.37
O=S	–0.01	–0.54	–0.01	–0.00	–0.01	–0.01	–0.00	–0.05	–0.01	–0.01		0.00	0.00	0.00	–0.00	0.00	0.00
TOTAL	99.2	99.8	100.9	100.9	98.5	100.9	100.3	99.2	100.1	100.4	0.1	99.8	98.7	98.5	98.9	100.7	101.0
$Fe_2O_3(T)$	1.75	2.31	1.27	1.86	12.2	6.04	0.60	10.7	0.82	0.29		0.64	0.24	0.39	1.41	0.56	0.40
S	300	10800	150	100	300	250	100	1000	150	150		nf	nf	nf	100	nf	nf
Be	1.1	0.9	7.7	0.4	1.0	3.6	0.5	1.5	1.4	1.1			1.2	6.2	8.2	2.6	2.4
Li	22	160	13	nf	3	86	nf	173	23	7		9	nf	56	8	14	15
B	55	38	23200	<25	40	160	<25	50	30	<25	95	55	400	6800	26100	8300	660
Sc	15.3	4.2	30.4	0.9	3.0	20.7	1.0	25.8	16.1	21.0	13.9	12.1	13.6	27.4	29.1	10.0	16.9
V	77	27	233	12	20	188	10	203	164	136		90	129	229	161	111	188
Cr	39	24	176	15	17	125	16	224	115	109	85	65	103	200	4	90	128
Co	1.8	5.0	2.6	3.1	20.3	17.1	0.6	38.0	2.7	1.3	10.0	9.1	1.0	0.6	3.7	1.6	1.1
Ni	36	31	428	nf	46	80	nf	69	87	178		91	55	44	92	32	14
Cu	89	1308	16	7	18	42	5	92	11	9		9	6	9	22	48	19
Zn	702	950	41	16	101	67	16	46	9	6		19	16	23	72	46	19
As	nf	56	nf	4	22	nf	3	30	nf	nf		48	11	7	nf	nf	nf
Rb	30	17	45	10	11	207	nf	86	55	nf		65	40	205	46	52	166
Sr	255	26	73	221	99	70	444	196	210	127		115	126	50	49	26	53
Y	29	4	21	13	38	14	12	17	15	28		26	18	20	22	6	8
Zr	113	17	198	56	51	140	58	103	88	117		99	109	177	206	97	136
Nb	15	3	25	16	10	14	16	4	16	18		11	14	24	17	11	14
Sb	1.9	43.0	2.1	3.0	7.4	2.2	38.0	2.0	2.3	2.2	1.6	4.3	8.1	4.4	2.4	1.5	0.9
Cs	0.9	2.5	2.7	0.7	1.2	15.8	0.4	6.9	3.0	1.5	1.5	6.9	2.6	11.0	2.1	1.9	13.1
Ba	25	17	73	21	49	458	18	70	66	54		100	64	518	126	133	350
La	7.6	4.1	4.0	7.7	27.4	39.7	6.8	8.1	3.8	5.9	21.2	42.1	27.8	7.6	19.0	3.0	4.9
Ce	21.9	9.0	6.3	16.0	47.2	81.4	6.9	19.5	8.3	11.7	56.1	105.0	69.5	17.6	37.0	6.4	11.1
Nd	13.7	3.9	4.8	9.5	26.3	33.6	5.7	11.7	6.6	10.2	31.9	41.5	34.0	11.8	19.3	3.2	5.2
Sm	2.82	0.82	1.34	2.27	8.19	5.25	1.41	2.75	1.98	3.79	9.44	7.70	5.74	3.57	5.06	0.67	1.00
Eu	0.54	0.14	0.37	0.70	3.61	0.88	0.33	0.87	0.29	0.30	0.60	0.80	0.25	0.29	0.38	0.12	0.16
Gd	3.7	0.0	1.8	2.4	8.0	4.4	1.2	nf	2.4	5.7	9.3	9.1	6.2	6.7	7.7	0.0	0.0
Tb	0.60	0.18	0.44	0.35	1.28	0.67	0.22	0.55	0.30	1.18	1.40	1.35	0.80	1.18	0.98	0.12	0.19
Tm	0.47	nf	nf	0.13	0.60	nf	0.07	0.31	nf	0.73	0.56	0.44	0.31	0.64	0.68	0.07	0.21
Yb	3.10	0.42	2.62	0.66	2.45	2.61	0.56	1.85	1.40	4.31	3.42	2.55	2.03	4.31	3.72	0.90	1.58
Lu	0.46	0.05	0.46	0.08	0.35	0.37	0.08	0.25	0.19	0.61	0.54	0.37	0.38	0.59	0.66	0.17	0.23
Hf	2.7	0.5	5.0	0.2	0.2	4.0	0.1	2.0	3.1	3.7	2.4	2.4	3.0	6.1	5.6	2.2	3.8
Ta	0.83	0.17	1.53	0.10	0.10	1.25	nf	0.42	0.97	1.13	0.80	0.76	0.89	1.85	1.92	0.70	1.10
Th	7.10	1.60	15.00	0.60	1.00	13.40	0.40	0.79	9.10	12.90	7.30	8.00	14.00	22.20	19.30	4.20	12.00
U	2.9	0.3	3.2	0.4	1.4	2.7	0.6	0.8	1.8	1.9	1.9	2.2	2.2	3.8	4.3	1.3	1.3
Pb	198	50000	138			15		52	13	10							

Table 4 *contd.*

SAMPLE	SC20B	SC21	47262	47263	47253	DH1	DH4	DH5	DH6	DH7	DH9	DH10	DH11	DHQ3	DHQ5	DHQ6
SiO_2	72.2	62.6	49.6	39.9	56.5	58.6	55.2	49.0	58.8	52.2	64.1	46.7	69.6	70.2	57.3	53.9
TiO_2	0.48	0.65	1.12	1.46	1.05	0.43	0.60	0.74	0.66	0.64	0.74	1.20	0.65	0.61	1.00	0.78
Al_2O_3	12.2	18.5	28.2	32.2	23.6	9.88	15.5	17.6	18.5	12.7	17.8	20.0	17.9	15.8	22.3	19.5
Fe_2O_3	0.20	0.60	0.07	0.20	0.16	0.69	1.00	1.43	0.81	2.45	0.83	1.54	0.49	0.00	0.72	0.35
FeO	0.56	0.17	0.32	0.39	0.13	6.99	3.38	4.29	6.13	6.87	2.09	10.5	0.10	0.26	3.10	2.93
MnO	0.05	0.03	0.02	0.02	0.02	0.09	0.09	0.14	0.05	0.59	0.04	0.04	0.01	0.02	0.05	0.06
MgO	2.70	0.45	5.02	6.43	3.54	3.71	2.13	4.15	2.33	5.07	2.02	5.96	0.07	0.36	2.10	2.94
CaO	1.09	3.24	0.25	0.38	0.42	6.79	4.33	5.21	0.30	5.92	0.19	0.78	0.12	0.72	0.94	3.74
Na_2O	0.61	8.95	1.27	1.64	0.78	0.11	7.35	0.35	5.35	1.96	8.78	3.74	8.91	9.92	5.73	6.77
K_2O	0.58	0.36	2.29	1.63	2.94	1.03	0.60	3.90	1.33	0.95	0.76	1.61	0.37	0.43	2.70	1.52
P_2O_5	0.05	0.11	0.09	0.24	0.16	0.06	0.16	0.13	0.13	0.09	0.13	0.21	0.02	0.09	0.19	0.15
H_2O^+	1.53	0.73	3.27	3.72	4.07	3.51	1.73	4.04	3.49	4.52	1.88	6.14	0.41	0.30	2.63	1.71
CO_2	1.43	3.07	0.87	0.22	nf	7.11	4.62	7.09	0.40	5.07	nf	0.98	0.12	0.86	1.39	5.57
others	3.30	0.26	6.91	9.48	3.83	0.19	0.15	0.44	0.19	0.18	0.17	0.41	0.10	0.08	0.24	0.18
O=S	–0.00	0.00	0.00	0.00	0.00	–0.00	–0.01	–0.10	0.00	0.00	0.00	–0.07	0.00	0.00	0.00	0.00
TOTAL	97.0	99.7	99.3	97.9	97.2	99.2	96.8	98.4	98.4	99.2	99.6	99.7	98.9	99.6	100.4	100.1
$Fe_2O_3(T)$	0.82	0.79	0.43	0.63	0.30	8.46	4.76	6.20	7.62	10.1	3.15	13.2	0.60	0.28	4.17	3.61
S	100	nf	nf	nf	nf	100	250	2000	nf	nf	<50	1500	nf	nf	nf	nf
Be	2.7	1.5	8.8	10.9	5.6	1.0	1.1	2.8	2.1			3.3			3.2	1.9
Li	13	3	37	41	27	128	73	82	149	143	64	238	4	1	63	42
B	9900	550	20800	28700	11400	50	<25	60	25	30	<25	55	30	<25	70	35
Sc	10.8	15.2	20.3	30.8	25.8	8.4	10.3	17.0	10.0	13.8	15.8	29.7	9.7	10.5	21.0	18.0
V	120	85	202	224	202	91	82	164	173	123	170	234	99	62	201	160
Cr	97	85	133	172	152	70	78	105	100	90	110	338	93	89	139	124
Co	2.7	0.5	0.7	1.1	0.9	22.2	12.6	18.5			35.5	46.5	1.5	4.8	25.2	22.1
Ni	32	14	44	24	45	91	26	133	101	94	81	147	35	32	113	113
Cu	16	11	9	12	8	63	20	33	16	36	6	9	6	3	8	8
Zn	44	41	17	18	16	91	27	74	74	92	18	47	28	1	120	24
As	34	nf	8	12	6	12	11	17	26	47	38		nf	27	29	18
Rb	23	nf	88	75	123	51	23	209	69	41	28	86	nf	13	108	65
Sr	37	166	47	55	40	128	140	95	66	164	111	107	208	129	110	233
Y	9	19	8	11	6	17	16	20	16	21	20	10	7	11	30	17
Zr	71	101	145	200	148	90	92	116	105	93	111	98	109	96	141	116
Nb	10	14	21	28	19	11	12	19	13	15	15	6	13	3	17	14
Sb	2.2	1.1	3.9	3.1	6.4	11.0	4.0	4.6	1.6	4.1	83.0	5.0		3.8	3.2	2.8
Cs	1.0	0.9	3.2	4.0	8.9	2.1	1.7	5.1	3.0	2.8	1.7	9.9		1.8	8.2	3.3
Ba	37	26	598	246	259	77	43	400	99	86	71	150		35	241	112
La	7.6	4.0	52.0	133.0	6.1	42.0	30.4	41.1	46.5	38.8	58.6	9.0		12.4	37.8	28.8
Ce	16.4	12.1	93.6	242.0	9.7	79.3	56.4	74.2	81.0	67.5	100.0	15.7		28.5	102.0	71.0
Nd	7.0	7.9	29.0	85.0	5.2	33.6	24.0	33.9	34.9	30.0	43.4	4.8		14.7	43.3	31.4
Sm	1.43	2.30	2.57	9.60	1.16	5.48	4.18	5.67	5.30	5.34	7.50	2.13		3.03	7.50	5.03
Eu	0.24	0.26	0.23	0.74	0.11	0.94	0.71	1.01	1.03	1.20	0.66	0.50		0.49	1.52	0.86
Gd	0.2	0.0	<2	5.2	<2	4.3	4.9	3.1	nf	nf	6.3	1.1		4.5	6.6	4.2
Tb	0.20	0.57	0.28	0.72	0.15	0.54	0.49	0.51	0.57	0.71	0.96	0.41		0.48	0.90	0.56
Tm	0.12	0.29				0.33	0.21	0.37	0.41	0.37	0.43	0.15		0.26	0.59	0.34
Yb	1.09	1.90	2.72	4.34	1.76	1.55	1.38	2.60	1.64	2.43	2.37	1.35		1.86	3.38	2.57
Lu	0.17	0.30	0.42	0.64	0.29	0.23	0.22	0.38	0.28	0.37	0.33	0.21		0.24	0.48	0.37
Hf	2.2	2.8	4.20	5.70	4.10	1.9	2.6	3.4	3.0	2.9	3.4	2.0	2.7	2.8	4.1	3.4
Ta	0.62	0.88	1.3	1.7	1.2	0.63	0.74	0.80	0.87	0.81	1.04	0.43		0.83	1.30	1.10
Th	9.90	8.40	15.30	22.00	15.40	6.80	8.70	10.50	11.60	8.40	11.30	0.78	8.90	8.40	13.20	10.90
U	1.0	2.0	2.90	3.60	1.30	1.7	1.7	2.4	2.4	1.9	3.3	0.9		1.3	2.8	2.5
Pb	86						19	39	119							

SAMPLE	DHQ7	DHQ8	DHQ9	DHQ10	DHQ11	DHQ12	PC5	PC6	ST1	ST2	ST5	TR1	TR2	TR3	CAT2	CAT3
SiO_2	66.5	67.9	48.8	58.0	87.6	42.9	60.4	41.2	53.2	47.4	62.7	45.3	59.9	57.7	56.6	47.7
TiO_2	0.55	0.63	1.55	0.92	0.49	1.40	0.71	2.76	0.87	1.74	0.79	2.59	0.87	0.81	0.88	2.00
Al_2O_3	16.9	18.6	15.4	20.7	6.32	15.9	14.6	14.2	24.4	17.8	19.6	10.6	23.3	21.8	22.0	16.7
Fe_2O_3	0.00	0.49	1.27	0.55	0.12	0.50	1.42	1.02	2.32	1.29	1.55	1.75	3.36	3.13	1.71	1.79
FeO	0.54	0.16	8.92	3.56	0.68	13.1	5.08	12.0	4.14	7.89	3.45	8.08	0.49	1.77	4.47	11.4
MnO	0.04	0.02	0.17	0.06	0.04	0.20	0.16	0.29	0.05	0.11	0.06	0.13	0.01	0.02	0.06	0.17
MgO	1.14	0.35	4.93	2.74	0.67	9.80	3.49	5.89	2.63	4.34	2.94	9.82	1.30	1.43	2.50	6.13
CaO	2.10	1.09	5.11	0.60	1.11	2.22	1.76	3.87	0.32	6.39	0.19	14.2	0.16	0.90	0.17	9.36
Na_2O	8.74	8.67	3.48	4.28	1.75	0.81	0.51	4.07	0.35	4.83	0.36	2.51	0.41	0.33	3.60	2.84
K_2O	0.40	0.60	1.05	3.50	0.94	1.39	3.30	0.49	6.19	0.44	4.43	0.16	6.24	5.33	3.13	0.15
P_2O_5	0.12	0.26	0.09	0.17	0.11	0.25	0.16	0.65	0.07	0.33	0.07	0.34	0.09	0.08	0.09	0.16
H_2O^+	0.22	0.53	4.31	3.28	1.01	7.21	4.37	4.73	4.95	4.16	4.32	2.45	4.12	4.59	3.99	2.07
CO_2	2.90	1.26	4.06	1.09	0.63	3.19	1.89	3.80	0.29	3.46	0.16	1.84	0.26	1.88	0.15	0.11
others	0.11	0.11	0.51	0.26	0.09	0.42	0.22	0.37	0.19	0.21	0.17	0.23	0.26	0.22	0.19	0.19
O=S	0.00	–0.00	–0.15	0.00	0.00	–0.06	0.00	–0.06	0.00	–0.00	0.00	0.00	0.00	0.00	0.00	0.00
TOTAL	100.3	100.7	99.5	100.2	101.0	99.2	98.0	95.2	99.9	100.4	100.8	100.0	100.8	99.9	99.6	100.8
$Fe_2O_3(T)$	0.57	0.67	11.2	4.51	0.88	15.1	7.07	14.3	6.92	10.1	5.38	10.7	3.90	5.10	6.68	14.4
S	nf	50	3000	nf	nf	1300	nf	1200	nf	50	nf	nf	nf	nf	nf	nf
Be		1.0	1.5						3.1	1.5	2.9	1.7	3.5	3.4	2.8	0.9
Li	1	5	84	67	14	239	88	181	99	117	102	29	20	40	112	69
B	<25	<25	<25	55	<25	30	75	<25	85	<25	60	<25	200	130	45	<25
Sc	13.0	8.8	31.4	21.8	8.1	29.9	15.7	21.0	19.4	21.8	17.5	67.0	20.6	20.3	22.3	35.4
V	102	86	181	198	82	232	109	204	133	245	119	309	264	182	208	313
Cr	94	118	216	130	97	567	93	102	121	14	104	98	128	130	128	168
Co	2.6	1.3	37.0	28.4	2.6	56.0	22.0	52.0	14.4	25.0	22.6	44.0	32.0	10.4	16.8	43.8
Ni	49	37	25	165	41	175	88	118	40	19	44	84	64	58	69	39
Cu	6	24	44	34	3	51	45	56	10	42	12	108	71	50	17	5
Zn	5	17	55	25	19	94	72	120	59	79	45	61	18	85	53	122
As	35	12	8	47	7	28	11	75	4	5	2	3	63	36	23	4
Rb	13	21	59	147	37	57	135	nf	224	28	193	nf	333	242	153	17
Sr	257	206	537	183	58	54	52	131	24	526	38	468	54	62	45	294
Y	17	27	17	19	6	11	13	30	19	19	11	17	16	13	16	19
Zr	77	108	79	147	78	95	113	225	139	19	133	156	106	112	118	127
Nb	10	11	6	20	9	nf	14	94	16	23	12	27	16	16	16	5
Sb	9.4	4.9	3.4	13.1	3.9	1.3	1.1	2.7	1.5	1.8	1.1	1.0	4.4	2.5	1.8	0.3
Cs	1.1	1.3	9.7	11.2	1.8	3.8	8.4	1.7	9.7	9.4	7.8	0.6	15.3	15.5	9.0	7.4
Ba	44	58	93	325	100	146	434	48								
La	3.8	3.6	6.7	47.2	9.7	6.5	39.4	73.2	50.5	15.1	36.0	24.5	44.1	51.9	47.0	9.6
Ce	15.1	13.1	17.9	94.5	24.7	15.3	84.4	141.0	92.6	31.4	71.5	54.0	89.6	100.0	92.5	20.7
Nd	13.2	10.0	12.4	42.3	14.6	9.4	34.1	55.4	35.4	16.1	31.7	31.8	41.0	38.3	38.5	16.4
Sm	3.24	2.88	3.21	7.77	2.48	2.70	6.20	9.70	5.74	3.82	5.19	7.49	6.79	5.37	5.85	4.00
Eu	0.42	0.52	1.17	1.38	0.28	0.60	1.32	2.63	1.15	1.54	1.04	2.47	1.12	0.84	1.24	1.70
Gd	0.0	5.3	0.0	7.0	nf	nf	5.6	7.7	6.9	2.2	5.1	5.1	4.7	5.0	6.1	3.7
Tb	0.48	0.80	0.64	1.01	0.24	0.58	0.74	1.08	0.79	0.63	0.67	1.03	0.78	0.55	0.62	0.71
Tm	0.25	0.44	0.33	0.62	0.16	0.27	0.35	0.61	0.39	0.16	0.35	0.27	0.35	0.39	0.39	0.35
Yb	1.69	2.72	1.90	3.46	0.88	1.78	2.54	2.45	2.92	1.56	2.49	1.42	3.02	2.42	2.65	1.82
Lu	0.21	0.38	0.27	0.49	0.11	0.22	0.33	0.31	0.40	0.22	0.36	0.16	0.45	0.35	0.36	0.27
Hf	2.5	2.7	2.2	4.1	2.2	2.0	3.7	6.5	3.5	2.8	3.8	5.4	3.7	3.8	3.9	3.1
Ta	0.64	0.90	0.41	1.07	0.64	0.37	1.00	5.80	1.10	1.20	1.00	2.00	1.20	1.00	1.00	0.50
Th	6.90	7.20	0.67	12.40	6.80	0.48	10.00	9.00	13.70	1.70	11.70	2.50	14.00	13.60	14.10	0.60
U	2.3	1.9	0.2	2.8	1.2	0.2	1.7	2.6	2.1	0.5	3.4	0.7	2.8	2.7	2.4	0.3
Pb									19	64	39	22	19	40		

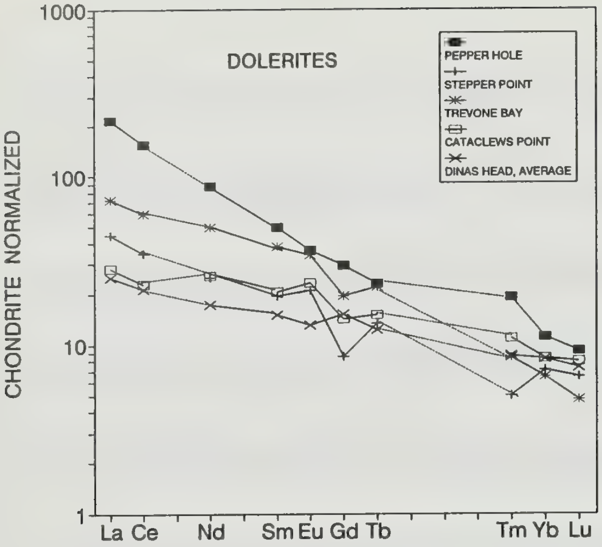

Fig. 4 Chondrite normalised REE plots for the dolerites. The Dinas Head plot is the average of six samples.

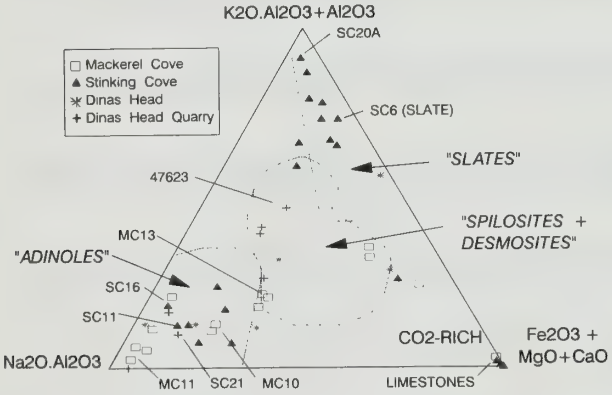

Fig. 5 Ternary diagram (modified after Agrell, 1939) delineating fields for 'adinole', 'spilosites + desmosites' and 'slate'. Samples plotted are all the Dinas Head sediments, and those labelled are referred to in the text.

field, albite is a major mineral phase, whereas mica and chlorite are predominant in sediments from the 'slate' field. It is also noteworthy that true 'adinoles' occur in all 4 sections sampled, illustrating the extensive distribution of adinoles at Dinas Head. Samples rich in CO_2 plot towards the (Fe_2O_3+FeO+MgO+MnO+CaO) apex of the ternary diagram.

Sediments from the Stinking Cove section appear to differ from those of the other sections in that they plot either as true adinoles (e.g. SC11 and SC16), or in the 'slate' field of the ternary diagram (e.g. SC20A, Fig. 5). All of the samples in the 'slate' field are boron-rich, although some adinoles at Stinking Cove are also boron-rich (e.g. SC21, NA_2O = 8.95%, B = 550 ppm), but with lower boron concentration levels. It appears likely that the introduction of boron was concomitant with removal of sodium.

The sample of unaltered fissile slate collected from the Stinking Cove section (SC6) plots well within the 'slate' field. Slate samples collected well away from the intrusive dolerites at Stepper Point (ST5) and Trevone Bay (TR3), also plot very close to the Dinas Head slate sample on all the geochemical diagrams presented (e.g. Figs 6, 10 and 11).

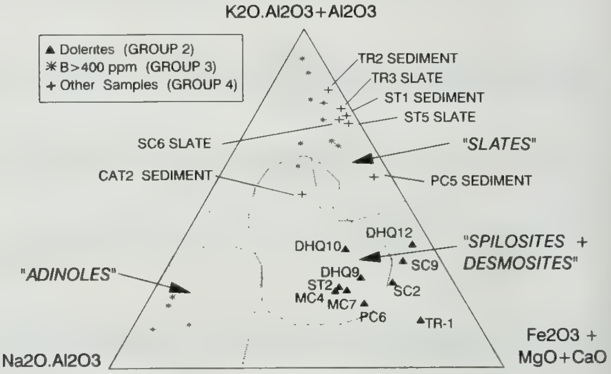

Fig. 6 Apices as for Fig. 5. Samples plotted are: dolerites — GROUP 2 (filled triangles); sediments with B>400 ppm — GROUP 3 (stars); sediments associated with dolerites from other N Cornwall localities (crosses).

Sediments associated with dolerites from Stepper Point, Pepper Hole and Trevone Bay do not show any chemical indications of adinolisation, and plot in the 'slate' field (Fig. 6). However, the sediment associated with the dolerite from Cataclews Point plots in the 'spilosite + desmosite' field, and may well indicate that some degree of sodium mobility had occurred.

Sediments with Na_2O >4%, i.e. those which plot in the 'adinole' or 'spilosite + desmosite' fields, were classified as GROUP 1 sediments in all following diagrams. The REE contents vary for this group, and are plotted as chondrite-normalised values in Fig. 7 in the field delineated by ±1 standard deviation of the mean of these values. In general, the GROUP 1 sediments are light-REE enriched with a prominent negative Eu anomaly. The unaltered slate (SC6) is shown for comparison in Fig. 7, and has a similar pattern to that of the GROUP 1 sediments, although REE concentrations are slightly higher than the GROUP 1 mean. GROUP 3 sediments, i.e. those with boron greater than 400 ppm, are similarly light-REE enriched, but generally with a larger negative Eu anomaly (Fig. 8). Sediments rich in CO_2 generally have flatter chondrite-normalised patterns, with positive, or less negative, Eu anomalies (Fig. 9).

All analytical data, including the dolerites, are plotted on Taylor and McLennan's (1985) ternary diagrams Hf-Th-Co (Fig. 10), and Th-La-Sc (Fig. 11), which are used to discriminate post-Archean sediments. The unaltered slates, together with those sediments in close proximity to dolerites *other than* the Dinas Head intrusion, plot within the post-Archean sedimentary fields on both ternary diagrams. These samples, together with the CO_2-rich sediments and the quartz-granite veins (SC2 and DHQ11), are classified as GROUP 4 samples. Many of the Dinas Head sediments however, plot outside the post-Archean sedimentary fields on both diagrams. In the Hf-Th-Co diagram, Fig. 10, the variation is greatest, as both GROUP 1 and GROUP 3 sediments plot on either side of this field. In the Th-La-Sc diagram, Fig. 11, the sediments are better delineated, with the majority of sediments in GROUPs 1 and 3 plotting within the post-Archean sedimentary field.

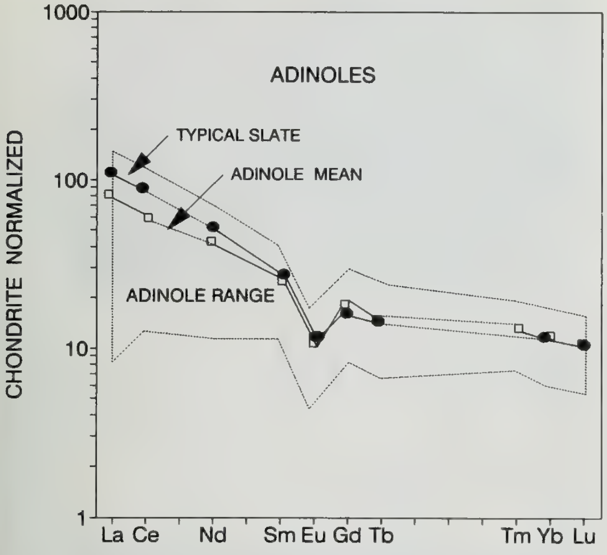

Fig. 7 Chondrite normalised REE plots for the range of adinoles from Dinas Head.

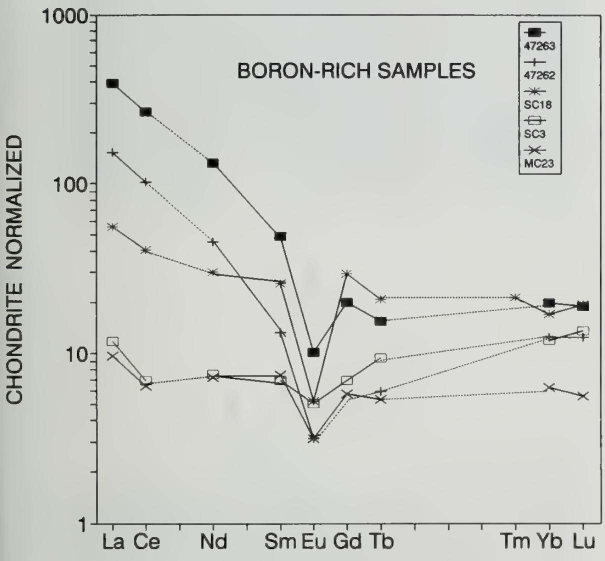

Fig. 8 Chondrite normalised REE plots for selected boron-rich sediments.

Samples plotting outside this field are predominantly boron-rich, and are relatively depleted in La.

The CO_2-rich samples at Stinking Cove (SC4, SC5 and SC7) plot together but separate from the other samples in the Th-La-Sc diagram (Fig. 11), and are distinct from the CO_2-rich samples at Mackerel Cove (MC5, MC6, MC8 and MC9). This difference is due to an enrichment of Sc (relative to La) which correlates with an observed greater abundance of Fe-carbonate (siderite) at Mackerel Cove.

In both ternary diagrams (Figs 10 and 11), the dolerites form a group which generally is distinct from the sediments.

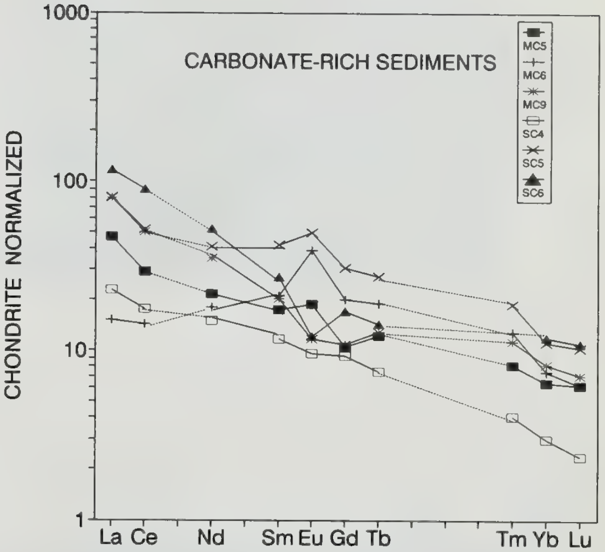

Fig. 9 Chondrite normalised REE plots for carbonate-rich rocks.

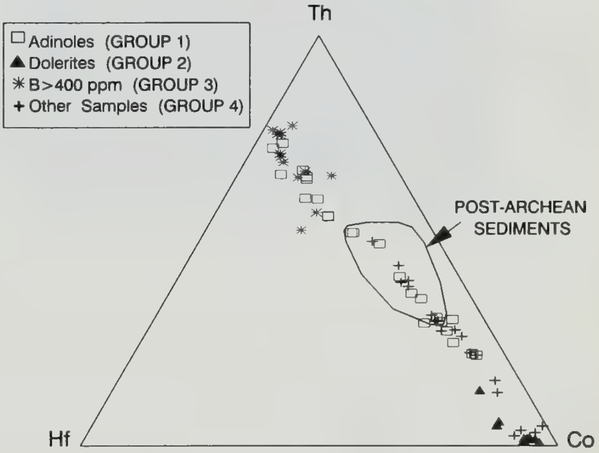

Fig. 10 Ternary diagram, after Taylor and McLennon (1985). Samples plotted are: adinoles — GROUP 1 (open squares); dolerites — GROUP 2 (filled triangles); sediments with B>400 ppm — GROUP 3 (stars); other samples — GROUP 4 (crosses).

Boron-rich samples

Agrell (1939, 1941) provides an excellent comprehensive textural and mineralogical description of the boron-rich samples from Dinas Head, where he identified dravite to be the sole boron-bearing mineral. Here, we analysed several samples using x-ray diffractometry and can confirm that dravite is the tourmaline mineral present. Our mapping of the sediments indicates that the boron mineralisation has a very localised areal distribution, as reported by Agrell (1939), and is confined to the top of the Mackerel Cove and Stinking Cove sedimentary sequences (Fig. 1). In thin section it was not possible to identify the tourmaline because of the small grain size of the minerals present; scanning electron microscopy showed the grain sizes to be typically less than 1 μm, Figs 3(c),(d).

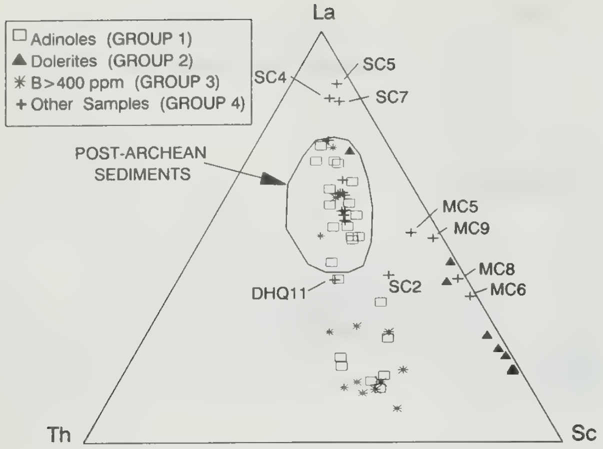

Fig. 11 Ternary diagram, after Taylor and McLennon (1985). Samples plotted are: adinoles — GROUP 1 (open squares); dolerites — GROUP 2 (filled triangles); sediments with B>400 ppm — GROUP 3 (stars); other samples — GROUP 4 (crosses).

In the ternary diagrams, Figs 6, 10 and 11, samples with boron concentration greater than 400 ppm are classified as boron-rich (GROUP 3). From the ternary diagram ($Na_2O.Al_2O_3$) – ($K_2O.Al_2O_3$) – (Fe_2O_3 + FeO + MgO + MnO + CaO), Fig. 6, originally used in Agrell's (1939) classification of adinoles, it can be seen that the boron-rich samples are not confined to any specific rock type, suggesting that the boron mineralisation post-dates the adinolisation metasomatic event. From the Th-La-Sc and Hf-Th-Co ternary diagrams, Figs 10 and 11, the boron-rich samples generally are depleted in Co, and to a lesser extent La, and a crude inverse correlation exists between these two elements and boron (Fig. 12). Chondrite normalised REE plots show a wide range for the light-REE, but are not significantly different from the boron-poor sediments, except generally to have larger negative Eu anomalies (Fig. 8). No significant correlations were observed for the other elements studied. Neither the dolerite nor the unaltered slate are enriched in boron and are unlikely to be the source for the mineralisation, and no boron-rich samples occurred with sediments associated with dolerites from the other areas in this study.

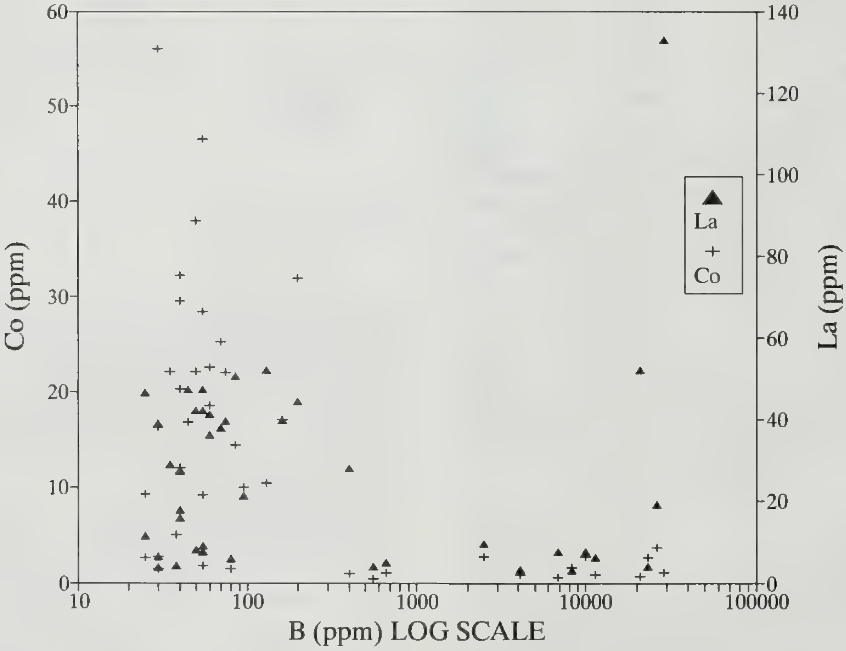

Fig. 12 B against La (filled triangles), and B against Co (crosses).

Boron Isotopes

The boron isotope signatures of an adinole sample from Stinking Cove (SC18), a tourmaline from Luxulyan, Cornwall (BM68598) and a colemanite (non-marine evaporite) from San Bernadino County, California (BM69058) were measured in an attempt to identify a source from which the boron may have been introduced.

The $\delta^{11}B$ value determined for adinole specimen SC18, referred to National Bureau of Standards boric acid SRM951 ($^{11}B/^{10}B$ ratio 4.04362, Catanzaro *et al.* (1970)) is 5.26‰. This value falls within the field of non-marine evaporites and at the low end of the ranges quoted for sediments and crustal rocks, as summarised by Palmer and Slack (1989). The $\delta^{11}B$ value of pegmatitic tourmaline from Luxulyan, Cornwall, was found to be 12.61‰ and that of the colemanite was found to be 5.13‰. Both lie broadly within the respective ranges for pegmatites and marine evaporites suggested by Swihart and Moore (1989) and Palmer and Slack (1989). According to the latter, seawater and marine evaporites are characterised by $\delta^{11}B$ of +20 to +40‰ whilst Swihart and Moore (1989) reported that pegmatitic tourmalines are depleted in the heavier isotope such that $\delta^{11}B$ is between 5 and 12‰.

Our limited data indicate that neither seawater nor marine

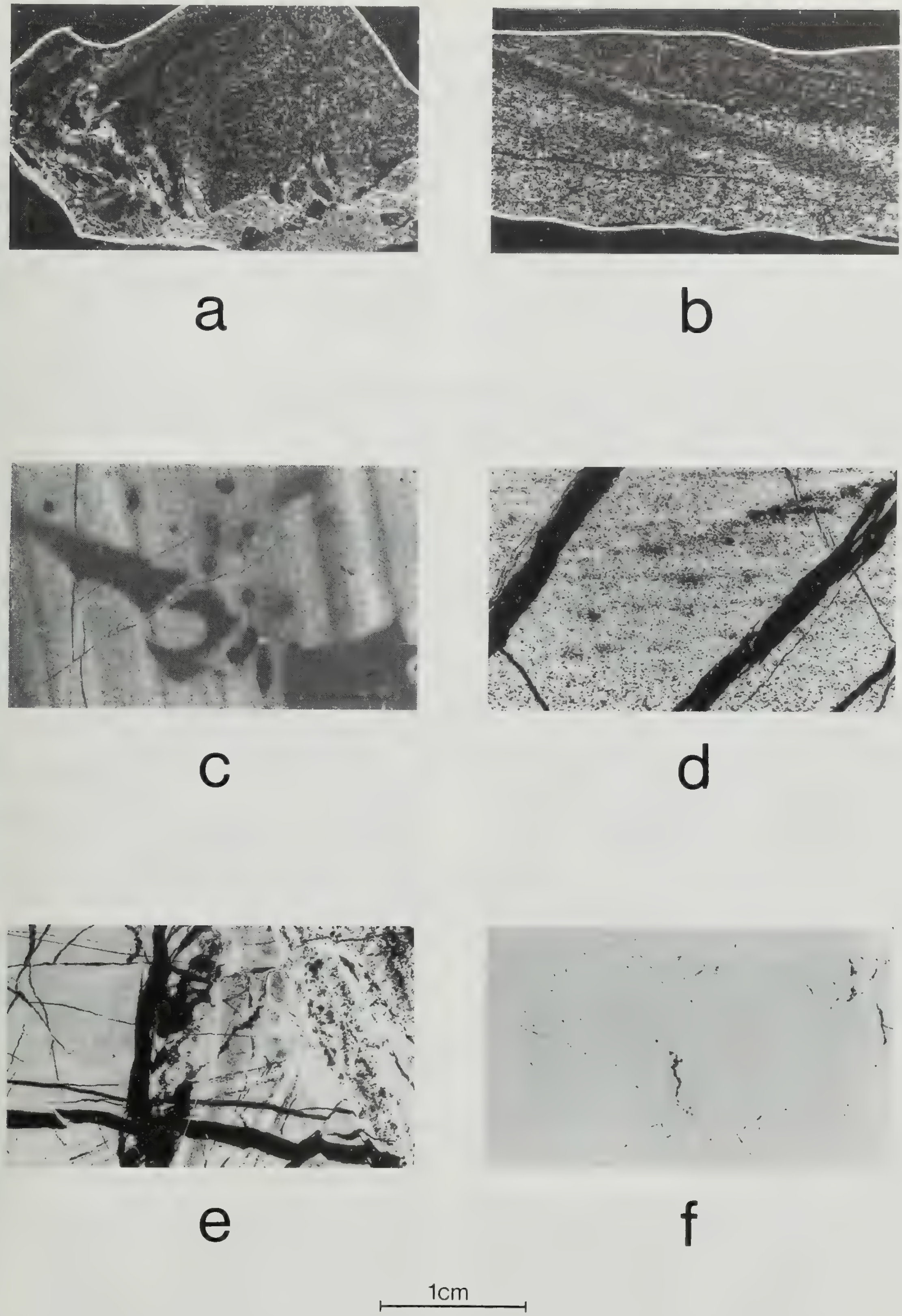

Fig. 13 Boron distribution maps of samples from Stinking Cove. (a) Sample number SC20A (660 ppm B); (b) SC17 (6800 ppm): (c) SC21 (550 ppm); (d) SC20B (9900 ppm); (e) SC19 (5300 ppm); (f) SC18 (25200 ppm).

evaporites could have been the source of the boron introduced during tourmalinisation of the rocks at Stinking Cove. Pneumatolytic fluids may have been involved but the measured ^{11}B depletion of the Cornish pegmatitic tourmaline is sufficiently greater than that of the adinole to indicate that this was not the case. None of the sediments that we examined from the area was found to contain boron at a concentration high enough to suggest that it may have been the source of the element.

Boron Mapping

Boron maps of six adinole samples are illustrated in Fig. 13. Usually, the boron, irrespective of its concentration, is homogeneously distributed throughout the bulk of the specimens, except where zones of post-tourmalinisation mineralisation occur. There is no evidence (such as boron-rich veins) to indicate the mechanics or pathways of boron ingress. Since the boron content of local unaltered slates is unexceptional (about 160 ppm, Shaw and Bugry, 1966) these rocks are unlikely to have been the source of the boron required for the tourmalinisation.

CONCLUSION

This study confirms Agrell's (1939) observations regarding the extensive areal distribution of adinoles at Dinas Head, north Cornwall. Albite-rich adinoles and spilosites extend from the most westerly point at Dinas Head through to the quarry section approximately 500 m east. The majority of samples studied in the Stinking Cove section showed, in addition to the Na-enrichment of normal adinoles, a significant degree of K-enrichment with mica and/or sericite being abundant. It is likely that a hitherto unrecognised phase of K-metasomatism had occurred together with the Na-metasomatism characteristic of adinole formation.

It was not possible to identify all the other elements affected by the adinolisation process because of the probable heterogeneous nature of the original sediments, and thereby lack of a control 'sample'. However, use of Taylor and McClennan (1985) discriminant diagrams for the elements Hf, Th, Co, La and Sc, and chondrite-normalised plots for the REE, indicate that La (and other light REE) were removed, and Th introduced during adinole formation.

It was not possible also to affirm or refute, from the geochemical and petrological data, the generally accepted view that the dolerite was the source of the Na (and/or K) in the formation of the adinoles. The chemical composition of the dolerite at Dinas Head is not significantly different from that of other dolerites in the area where adinoles were *not* observed at the dolerite/sediment contacts. However, the plagioclase present in the Dinas Head dolerite proved to be near end-member albite, some of which appeared to be primary in origin, and may well therefore have been associated with the adinolisation process.

Boron-rich samples, with boron in excess of 2%, were observed locally at Dinas Head, being restricted to the upper regions of the Stinking Cove section, and to the top of the Mackerel Cove section, close to a major fault zone cutting the northern part of the sequence. Dravite was identified as the sole boron mineral. The source of the boron was not identified, but it was unlikely to have been either the dolerites or the unaltered shales. Boron isotope data were inconclusive, indicating neither sea-water nor marine evaporites as the source of the boron. The isotopic ratio of a tourmaline from a Cornish pegmatite was also significantly different from that of the boron-rich sediment at Dinas Head.

The data presented here, and conclusions reached, are not in disagreement with Agrell's (1939) original hypothesis regarding formation of the adinoles at Dinas Head by metasomatic fluids emanating from the dolerite. We were not able however, to confirm this hypothesis. In addition, our observations are consistent with Agrell's (1941) hypothesis of tourmaline formation as a separate event, later than the adinolisation process. Thus while we were not able to ascertain conclusively the precise mechanisms of Na, K and B metasomatism at Dinas Head, this study provides a useful database against which studies of rocks of a similar nature can be compared.

Acknowledgements. We are very grateful to Dr. R.C. Scrivener (British Geological Survey, Exeter) and Dr. A.M. Clark (The Natural History Museum, London) for comments on an earlier manuscript.

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Productellid and Plicatiferid (Productoid) Brachiopods from the Lower Carboniferous of the Craven Reef Belt, North Yorkshire

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Synopsis. Lower Carboniferous, mainly Asbian, productoid genera, assigned to the closely related families Productellidae and Plicatiferidae, are described from reef limestone facies in the Craven Reef Belt of North Yorkshire and elsewhere, together with discussions on their relationships to genera abroad. Within the Productellidae the evolutionary history of species of *Productina* and *Argentiproductus* is described, while in the Plicatiferidae species of *Plicatifera, Acanthoplecta, Admodorugosus* gen. nov. (based on the type species *A. cracoensis* gen. et sp. nov.) and *Geniculifera* are described. The little-known British latest Devonian to earliest Carboniferous genus *Productellina* is placed in the Productininae, as is also a new Mongolian late Devonian genus, *Dorsirugatia*, described in the Appendix.

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INTRODUCTION

Brachiopods are an important biotic component of the late Viséan (largely Asbian) Cracoean reefs (see Brunton & Mundy, 1988*b*) of northern England, with productidines (represented by some 45 genera) forming 37% of brachiopods in detailed collections of almost 21,000 specimens from the Craven Reef Belt made by Mundy (1980). Contributions to the systematics, palaeoecology and distribution of some of these Cracoean productidines have been made by Brunton & Mundy (1986, 1988*a*, *b*) and Mundy & Brunton (1983, 1985).

Here we describe contemporaneous taxa belonging to the families Productellidae and the related Plicatiferidae, with species assigned to *Argentiproductus, Productina, Plicatifera, Acanthoplecta, Geniculifera*, and the new genus *Admodorugosus* (p.111). Some of these species, including *Acanthoplecta mesoloba, Plicatifera plicatilis, P. pseudoplicatilis* and *Argentiproductus margaritaceus* are familiar, if not diagnostic components of the reef biota, while the remaining are rare, poorly known or overlooked. *Argentiproductus atripoides*, a Russian species, is recognized for the first time in Britain, as is the North American genus *Geniculifera*, here accommodating *Productus keyserlingianus* de Koninck, which formerly was loosely referred to *Avonia*. A rare productellid in the Cracoean biota is *Productina* cf. *pectinoides*, providing an opportunity to redescribe the species and the difference between *Productina* and *Argentiproductus*. In so doing we have investigated the evolution of the small subfamily Productininae and its probable origins in the late Devonian genus *Dorsirugatia* and slightly younger *Productellina*. The distinctive wholly rugose plicatiferid *Admodorugosus cracoensis* gen. et sp. nov. is described herein; it is a rare component in our collections from the Craven Reef Belt, but has turned up in several museum repositories from a variety of Cracoean reef localities in England, Wales and Ireland.

A brief introduction to the stratigraphy and depositional setting of the Craven Reef Belt, together with definitions of the subfacies, is given in Brunton & Mundy (1988*b*). This paper also outlined possible pathways in productidine ontogeny with a notation which, used here, would be 1 to 3 to 5 for all species, that is from an initial pedicle attachment, via varied uses of clasping spines, to support spines in adulthood (Brunton & Mundy 1988*b*: fig. 4).

Although this study is based on the extensive collections made by Mundy from the Craven Reef Belt, we have made use of specimens from elsewhere in northern England, and beyond, in order to describe and illustrate the species more fully. Numerical and distributional data on the species here considered, together with their stratigraphical ranges (in the Craven Reef Belt) are shown in Table 1 (p.116) and Fig. 72 (p.117) respectively.

Most of the collections made from the Cracoe–Burnsall section of the Craven Reef Belt by Mundy (1980) are housed in The Natural History Museum, London (NHM), formerly the British Museum (Natural History), London, with additional material in the Liverpool Museum (National Museums & Galleries on Merseyside — NMGM). Collections by Mundy from the Malham–Settle portion of the reef belt during the resurvey by the British Geological Survey (BGS) Settle map-sheet (60) (Arthurton *et al.* 1988) are housed at Keyworth, Nottingham. Additional specimens of the species described here have been studied from existing collections (largely reef limestones) in The Natural History Museum, the British Geological Survey, the Sedgwick Museum, Cambridge, the Sheffield City Museum, and the Museum of Natural History, Paris. All the figured material, unless otherwise stated, is in The Natural History Museum, London, prefixed BMNH, followed by the registration number.

TERMINOLOGY AND CLASSIFICATION

Terminology follows the *Treatise* (Williams *et al.* 1965), but we use the following new or emended terms which are not defined by Muir-Wood & Cooper (1960) or the *Treatise* (1965):

Marginal ridges — Shell thickenings forming ridges bounding the body cavity and separating it from the ears and trail. They may include cardinal or lateral ridges, ear baffles and anterolateral subperipheral rims.

Body cavity (emended) — The main space between the valves which housed the posterior coelomic space plus the anterior mantle cavity accommodating the lophophore.

Cardinal ridges — Paired ridges extending from the cardinal process laterally along the dorsal hinge line.

Lateral ridges (emended) — Paired ridges extending from the cardinal process laterally which diverge from the dorsal hinge line.

The classification here used is not as in the *Treatise* (1965) because we find inconsistencies and difficulties in the use of that system. A new classification for the Productida is being developed by Brunton and Lazarev for use in the revised brachiopod *Treatise* now in preparation. Genera with true interareas, such as those included in the 1965 *Treatise* as Chonopectinae, will be moved from the previous Productellidae to the Strophalosioidea. Here the Productininae is moved from the *Treatise* Leioproductidae (which have deep body cavities and lack complete ribbing) to the Productellidae; the Plicatiferinae, within the *Treatise* Overtoniidae, is elevated to a family which includes the Levitusiinae, previously assigned to the Dictyoclostidae (the latter family now restricted to genera with a clear reticulate oramentation on the visceral disc).

SYSTEMATIC PALAEONTOLOGY

Synonymy lists are those involving significant taxonomical revision or major descriptions.

Superfamily PRODUCTOIDEA Gray, 1840.

DIAGNOSIS EMENDED. Productidines lacking true interareas. Cardinal process is posteriorly or posterodorsally directed. Commonly costellate with long trails (in younger taxa) and simple spines principally on ventral valves.

Family PRODUCTELLIDAE Schuchert, *in* Schuchert & Le Vene 1929.

DIAGNOSIS EMENDED. Small to medium sized productoids with shallow to moderately deep body cavities. Teeth only in Devonian genera. Ribbing variably developed or lacking, rugae weak or lacking. Spines few, on ventral valve only.

COMMENT. In the revised *Treatise* this family is to be expanded to include at least six subfamilies, each containing several genera. It is the oldest non-ribbed family in the evolution of the Productoidea, appearing in the Emsian, but varied ribbing developed in a few subfamilies, such as the Productininae late in the Devonian. The Leioproductidae differ mainly in having deep body cavities.

Subfamily **PRODUCTININAE** Muir-Wood & Cooper, 1960.

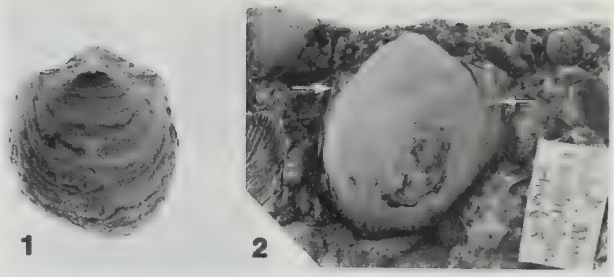
DIAGNOSIS EMENDED. Productellids with ribbing more strongly developed on ventral valves and lamellae on dorsal valves; few spines on ventral valve flanks only. Lateral ridges in both valves.

DISCUSSION. In the 1965 *Treatise* (Williams *et al.*) this subfamily contained two genera, *Productina* Sutton, 1938 and *Argentiproductus* Cooper & Muir-Wood, 1951. Brunton (1966) synonymized the two, principally because of their closely similar dorsal valve interiors. Since then several new species belonging to this group have been described from Lower Carboniferous rocks around the world, but mainly from Australia (Roberts 1976), Russia (Nalivkin 1979) and North America (Carter 1988, Rodriguez & Gutschick 1968).

Some authors (e.g. Carter, 1988) continued to recognize both genera and we now also differentiate two groups of species, attributable to *Argentiproductus* and *Productina*. The rather globose, small and relatively finely ribbed type species of *Productina, P. sampsoni* Weller, 1909 is mid Kinderhookian to early Osagian (mid to upper Tournaisian) in age, while the transverse, gently convex *Argentiproductus* type species, *A. margaritaceus* (Phillips, 1836) is from upper Viséan strata.

The earliest representative of the subfamily is probably the newly described late Devonian genus *Dorsirugatia* (Lazarev 1992, but see also Appendix, p.117, herein and listing in 1990 by Lazarev) from Mongolia. This is an inflated, but not deep-bodied, species with weak ribs not originating at the umbo, with a slightly rugose and lamellose dorsal valve, and few spines on the ventral valve only. Previously the earliest described species was *Argentiproductus rjausakensis* Nalivkin, 1979, from the uppermost Devonian of the southern Urals, closely followed by *A. dobroljubovae* Nalivkin, 1979 from the early Tournaisian of the Urals. These species are transverse in outline, with well developed ears, like *Argentiproductus,* but while the former appears to lack major spines, *A. dobroljubovae* has flanking spines. Thus it may be that here we have the last species of *Dorsirugatia* and, with the acquisition of strong spines, the first species of true *Argentiproductus*. At about the same time in North America are found specimens of *A. auriculatus* Carter, 1988, while species belonging to *Argentiproductus* extend into the Namurian, as in Algeria (Pareyn 1962).

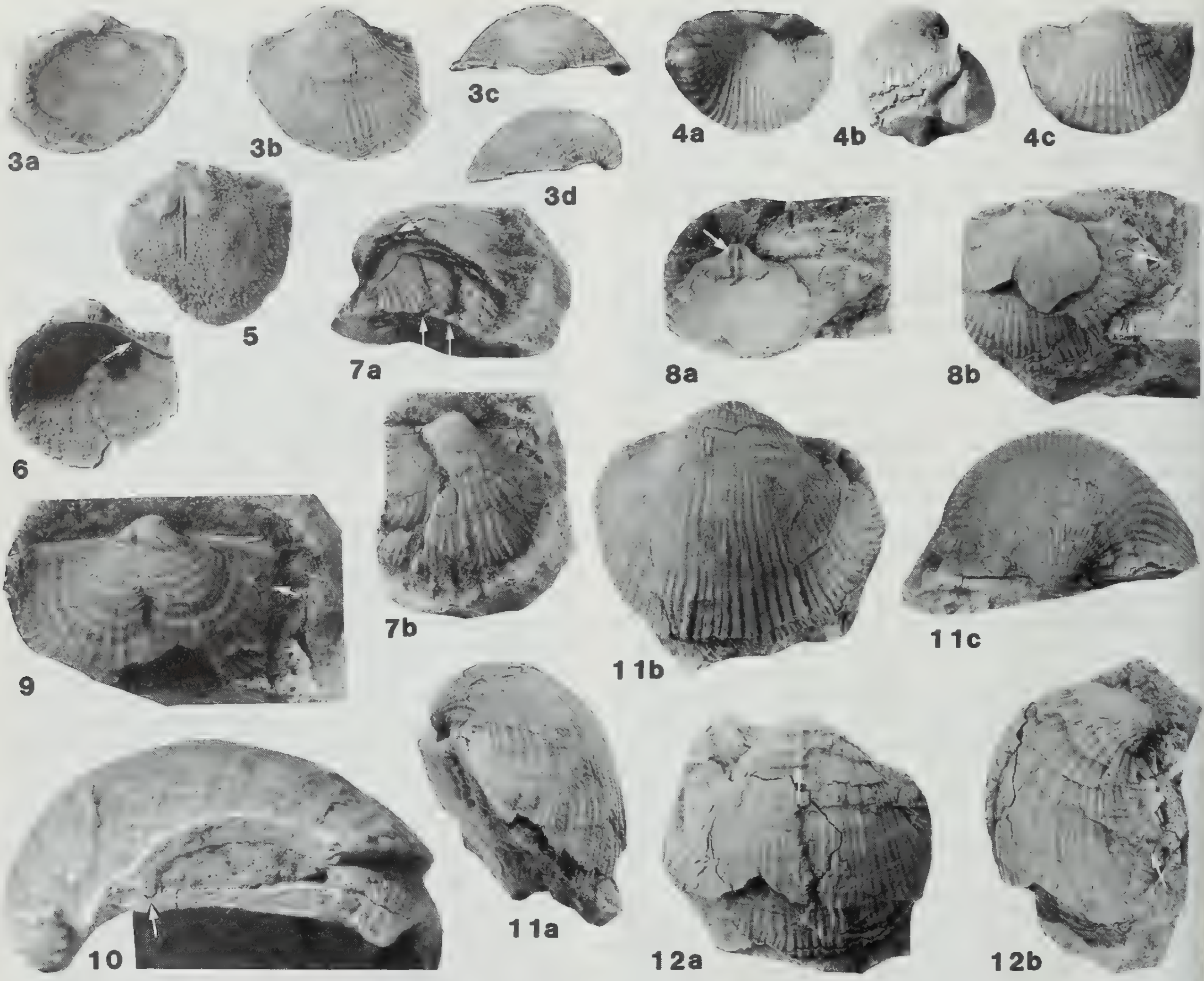
The poorly known genus *Productellina* Reed, 1943, which has not previously been photographically illustrated, is based on two specimens of *P. fremingtonensis* Reed from the Pilton beds of north Devon. Goldring (1970) described the Fremington section in north Devon and recorded this species from his faunal divisions B and C, equated with the *Gattendorfia* and *Ammonellipsites* zones respectively. It seems, therefore, that *Productellina* appeared in the early Hastarian, Lower Tournaisian. Study of the two types in the Sedgwick Museum, Cambridge, reveals that this genus belongs in the Productininae. Its elongate outline, dorsal valve lamellae (Fig. 1), rather fine ventral ribbing and apparently single pair of flanking spines (Fig. 2) indicate an affinity with *Productina*. *Productellina* differs from *Devonoproductus* by apparently lacking spines over the entire ventral valve. As a member of the Productininae it is probably only slightly younger than *Dorsirugatia*. Thus we have an early division in this subfamily into two lineages of species; *Dorsirugatia* evolving into *Argentiproductus* while *Productellina* evolved into *Productina*.



Figs 1, 2 *Productellina fremingtonensis* Reed, from the Pilton Beds of Fremington, north Devon, probably of lowest Tournaisian age. Specimens in the Sedgwick Museum, Cambridge. Fig. 1, latex mould of the dorsal valve exterior of the holotype described by Reed (1943) and figured by Whidborne (1898: pl. 22, fig. 2). E287, ×2. Fig. 2, internal mould of a ventral valve showing weak ribbing and the internal openings of paired spines (arrowed). H1665. x2.

In the mid Tournaisian of North America other elongate, weakly spinose and finely ribbed species evolved as *Productina sampsoni* Weller, 1909, and in late Tournaisian rocks *Productina parvula* Winchell, 1863 appears. The genus continued through the Viséan and, if the record of Winkler Prins (1968) of *P. pectinoides* (Phillips) is correct, the youngest record is from the early Bashkerian in north Spain.

The growth of long thin dorsal trails in this subfamily is characteristic. There is no evidence so far of ventral lamellae being as long, but we would not expect this. Dorsal valve growth involved no geniculation, but at all growth stages, after a length of a few mm, a short simple trail was composed of the margins of both valves. In order to accommodate the growing internal organs the geometry of the shell curvature necessitated periodical mantle regressions followed by rapid forward regrowth within (ventral to) the previous inner shell surface. In this way a series of long thin lamellose trails grew on dorsal valves. Each successive trail, although ventral to the last, allowed the new growth position to increase the depth of the body cavity slightly. Some of these lamellae grew to 10 mm or more in length, and as they became trapped in sediment they prevent easy extraction of dorsal valve exteriors. Thus dorsal valves are commonly found as exfoliated interiors. Although these dorsal trails grew as a consequence of shell geometry the survival advantage of this growth may have been two-fold. First, in the ability to maintain marginal trails during ontogeny which maintained a long narrow slit through which sea-water entering the mantle cavity could be monitored and 'filtered' (see Brunton, 1982, 1985); and secondly, in providing some protection to the dorsal valve against boring organisms. Brunton (1966) showed that in *Argentiproductus margaritaceus* only about half as many dorsal valves were bored as compared to ventral valves.



Figs 3–12 *Argentiproductus margaritaceus* (Phillips). Figs 3a–d, **neotype** (here selected), from Bishop's Quarry, Llandudno, north Wales, early Brigantian. Illustrated by Muir-Wood & Cooper (1960: pl. 123, figs 15, 16). Viewed dorsally, ventrally, posteriorly and laterally. BB13616.×1. Figs 4a–c, posterior, lateral and ventral views of a ventral valve exterior from near Mold, north Wales, showing characteristic ribbing and the paired flank spines. BB58627. ×1·5. Fig. 5, a dorsal valve interior from the same locality. BB58630. ×1·5. Fig. 6, a ventral valve interior from the same locality, showing the lateral ridge (arrowed). BB58629. ×2. Figs 7a–b, an incomplete shell with part of the ventral valve missing, showing the shallow body cavity (arrowed) and the lamellose nature of the dorsal valve exterior (arrowed). Stebden Hill. BD1643. ×1·5. Figs 8a–b, ventral valve exterior showing, at the exfoliated umbo, the internal mould of the ventral adductor muscle scars (arrowed), and the principal spine positions (arrowed). Stebden Hill. BD1645. ×1. Fig. 9, a ventral valve exterior showing growth deformation and spine bases (arrow); the shell damage results in a somewhat less inflated umbo than is typical for the species. This is a rare example from the framework facies. BD1634. ×1·5. Fig. 10, a shell from near Mold, north Wales, with one ear missing and showing the ventral lateral ridge fitting against the slight dorsal lateral ridge (arrowed). BB58628. ×5. Figs 11a–c, an example of the large form, viewed laterally, ventrally and posteriorly, from Parkhouse Hill, Derbyshire. B53583. ×1. Figs 12a, b, ventral and posterolateral views of a large specimen showing the somewhat lamellose nature of the valve surface and spine bases (arrowed). Caldbeck, Cumberland [Cumbria]. Natural History Museum (old collection) 75348. ×1.

Genus ***ARGENTIPRODUCTUS*** Cooper & Muir-Wood, 1951.

1928 *Thomasia* Fredericks: 790.
1931 *Thomasina* Paeckelmann: 181.
1942 *Thomasella* Paul: 191.
1951 *Argentiproductus* Cooper & Muir-Wood: 195.
1965 *Argentiproductus* Cooper & Muir-Wood; Muir-Wood: H471.
1966 *Productina* Sutton; Brunton: 208.

TYPE SPECIES. *Producta margaritacea* Phillips (1836: 215; pl. 8, fig. 8), by original designation of Cooper & Muir-Wood, 1951.

DIAGNOSIS EMENDED. Outline is hemispherical; profile is gently concavoconvex with short trails. Ribbing entire but variable, widening anteriorly. Lamellose, especially dorsally. Supporting spine rows extend from umbo across flanks, spines rare anteromedially. Short lateral ridges in both valves.

Discussion. The genus was placed in synonymy with *Productina* (Brunton, 1966) because the dorsal valve interiors of *Productina sampsoni,* figured by Muir-Wood & Cooper (1960: pl. 123, fig. 9) resembled extremely closely the dorsal interior of *A. margaritaceus.* The figure in Muir-Wood & Cooper (1960: pl. 123, fig. 17) purporting to be of *A. margaritaceus* is not of this species nor, we think, the genus; it may well belong to the linoproductids. The proliferation of more recently described species within the subfamily allows discrimination to be made between the two genera. *Argentiproductus* is commonly 20 to 25 mm wide across the body cavity (i.e. excluding ears). At a distance of 10 mm from the umbo about 6 to 10 ribs occur in 5 mm width; they are closely spaced, with flat to gently rounded crests. Because the ribs widen anteriorly and branch rarely, the number of ribs per unit width is variable. However, the ribbing on *Productina* species is finer, with rounded crests, and is more even over the entire shell. *Productina* is less wide but has a more strongly inflated ventral umbo giving steep flanks and a more strongly convex lateral profile than *Argentiproductus.* Spines are confined to ventral valves, but those on *Argentiproductus* are more prolific. Juvenile clasping spines (see Brunton, 1966) normally formed a ring just anterior to the initial point of pedicle attachment, the pedicle sheath, at about 0·5 mm from the tip of the umbo (Figs 13a, b). Thereafter a line of increasingly large support spines grew towards the anterior edges of the weakly defined ears, to a total of about six on each side. In addition the type species, and others in the genus, have one to three spines close to the mid-line, commonly only posteriorly, but rarely anteriorly also. Spines in *Productina* are confined to a few in each flanking row and are rare or lacking medially.

Argentiproductus margaritaceus (Phillips, 1836)

Figs 3–15

1836 *Producta margaritacea* Phillips: 215; pl. 8, fig. 8.
1861 *Productus margaritaceus* (Phillips); Davidson: 159; pl. 44, figs 5–7.
1960 *Argentiproductus margaritaceus* (Phillips); Muir-Wood & Cooper:182; pl. 123, figs 11–16.
1966 *Productina margaritacea* (Phillips); Brunton: 209; pl. 8, figs 1–19, pl. 15, figs 1–8.

Diagnosis. *Argentiproductus* with well defined, but not strongly convex, ventral umbo and a concavoconvex profile with a shallow body cavity. Spines include one medially at about 10 mm from umbo. Dorsal and ventral adductor scars slightly raised.

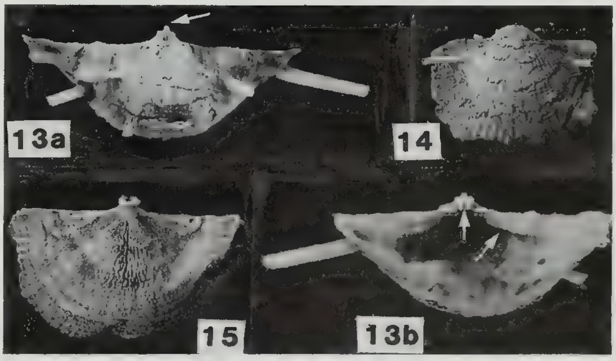
Type specimen. Neotype BMNH BB13616, here selected (Figs 3a–d), one of the specimens of *A. margaritaceus* (Phillips) selected by Muir-Wood to illustrate the genus and species in Muir-Wood & Cooper (1960); figure repeated in the brachiopod *Treatise* (1965). From the Bishop's Quarry Limestone, Bishop's Quarry, Llandudno, north Wales; the British Geological Survey Memoir (Warren *et al.* 1984) gives the age of this limestone as P_{1c}, early Brigantian. See Discussion, below.

Material. There are 64 specimens collected from the Craven Reef Belt by DJCM housed in the NHM and Liverpool Museum [NMGM]. Other specimens are from the Davidson and general collections at the NHM, including specimens from Bishop's Quarry, and the Sheffield City Museum. The large form is known from reef facies such as at Parkhouse Hill, Derbyshire and near Caldbeck, Cumbria. [The Caldbeck locality specimen in the NHM collections (75348) is recorded as from 'Falls Brew, Caldbeck', but we think this probably should be the locality Faulds Brow where quarries in high Viséan rocks were known. Both the specimen and its lithology indicate that reef facies are present in this area].

Age. Late Asbian and early Brigantian, late Viséan.

Discussion. Unlike most of the brachiopods described and figured by Phillips (1836) which were collected by William Gilbertson of Preston, this species was collected by Phillips himself while staying with Lord Cole (Sir P. Egerton) at Florence Court in County Fermanagh, Ireland, following the British Association meeting in Dublin of 1835. Although much of the Phillips collection is at the Oxford University Museum, examples of *A. margaritaceus* in that museum match neither the original Phillips illustration nor the refiguring of the specimen by Davidson (1861). An Oxford specimen, E2532, is undoubtedly conspecific, but is a representative of the larger form and about one-third larger than Phillips' illustrated specimen. The documentation with this specimen is sparse and there is some doubt as to whether it even originated from Phillips. For these reasons we have selected as neotype specimen one which well characterizes the common concept of the species and which the author of the genus herself selected to illustrate *Argentiproductus margaritaceus.* The neotype, when complete, would have been almost exactly the size of the Phillips specimen, as refigured by Davidson (1861), who pointed out that Phillips' illustration was somewhat enlarged.

A. margaritaceus is a variable species, especially in relation to its size and ribbing. The vast majority of specimens reach a maximun body width of about 25 mm, but a few rare specimens grew much larger, reaching about 40 mm across their visceral regions (Figs 11, 12). This gigantism is another example of the phenomenon discussed in *Antiquatonia* and



Figs 13–15 *Argentiproductus margaritaceus* (Phillips). Three silicified specimens from Asbian limestones near Derrygonnelly, Co. Fermanagh, Ireland. Figs 13a–b, posterior and anterodorsal views of a juvenile specimen showing the pedicle sheath (arrowed) and ventral lateral ridge (arrowed). Juvenile spines are well displayed. BB52916. ×6. Fig. 14, a ventral valve exterior showing the lamellose shell and spine positions. BB52907. ×2·3. Fig. 15, a young dorsal valve interior. BB52909. ×1·5.

Plicatifera by Timms & Brunton (1991), and is discussed further under *Plicatifera* herein (p.108).

The ribbing is characteristic in its anterior widening, rather flat-topped ribs and narrow interspaces. The density of ribs is very variable on any individual after a growth length of about 10 mm. The lamellose nature of the shell, especially of the dorsal valve, affected the height and dichotomy of ribbing. Rib dichotomy commonly occurred immediately posterior to a lamella, but anteriorly the two ribs commonly reverted to a single rib. As the shells grew so the rib width increased, by up to a factor, in adulthood, of about five times the early rib width (Fig. 4c). This expansion factor is even greater in the rare large specimens (Fig. 11b). The rib variability in association with lamellae and their variable increase in width results in inconsistent results of rib counts per unit width.

Internal morphology of the dorsal valve was described briefly by Muir-Wood & Cooper (1960) and of both valves by Brunton (1966). Noteworthy features are the lateral ridges in both valves diverging from the hinge lines (Figs 5, 6, 13b & 15). At early stages in ontogeny these ridges were built on earlier lines of prominent tubercules, and in adulthood they aided articulation, the ventral ridge fitting closely behind that of the dorsal valve (Fig. 10). Also in both valves the adductor muscle scars are raised and the internal surfaces of the valves, especially anteromedially, are strongly tuberculate. The dorsal median septum developed relatively late in ontogeny, never supported the cardinal process, but extends about 60% of the adult valve length. The cardinal process is sessile with a convex internal (ventral) surface from which the pair of grooved myophores converge dorsally in a V-shape.

The specimens described by Brunton (1966) as *P. margaritacea* are from rocks about 12 miles from Florence Court, the type locality, and both localities are considered as being of virtually the same Asbian age. These specimens are silicified and display external and internal morphology exceptionally well (see Figs 13–15); we believe that they represent the species, and thus the genus, particularly well.

The species is not common but occurs in western Europe more frequently in association with 'reefal' facies. Brunton (1985), based on initial work by Mundy (1980), described its distribution and that of *A. atripoides* (Gladchenko) on Stebden Hill, North Yorkshire. *A. margaritacea* is recorded in Europe, such as from the Viséan of Belgium (de Koninck 1847), the Brigantian of Poland (Zakowa 1985) and from the early Namurian of Kirghizia (Galitskaya 1977). It occurs also in the early Namurian of the Algerian Sahara (Pareyn 1962) and from mid Viséan rocks of northwest Australia (Roberts 1971).

Argentiproductus atripoides (Gladchenko, 1955)

Figs 16–21

1939 *Productus (Thomasina ?) atrypoides* Rotaï : 470 [466] (nomen nudum).
1955 *Productus (Thomasella) atripoides* Rotaï, 1937 (in litt.); Gladchenko: 13; pl. 1, figs 1–3.
1960 *Productus (Thomasella) atripoides* Rotaï, 1937 (in litt.); Gladchenko: 55; pl. 1, figs 1–3.
1977 *Productina atrypoida* (Rotai, 1963); Galitskaya: 27; pl. 5, figs 5–10; pl. 6, figs 9, 12.
1983 *Productina* (?) *atrypoida* (Rotay, 1939); Aizenverg: 77; pl. 41, figs 7, 8.
1985 *Productina* sp. undet., Mundy & Brunton: pl. 1, fig. 5.

DIAGNOSIS. Large *Argentiproductus*, rounded in outline, with almost flat valves (giving a very shallow body cavity), commonly distorted by hard substrate.

TYPE SPECIMEN. Lectotype, selected Aizenverg (1983), in the Leningrad (St Petersburg) Museum of F. N. Tchernyschew, collection N 5533, specimen 33; from Starobeshevo, Donbass, Upper Serpukhovian D_1 limestone = Arnsbergian.

MATERIAL. There are 31 specimens from the DJCM collection from Stebden Hill and one specimen from Elbolton (25 in the NHM and 7 in the Liverpool Museum). There are two specimens in the general collections of the NHM, one from Glutton, near Longnor, Derbyshire and the other from Treak Cliff, Derbyshire; all appear to be from reef framework facies. A single NHM specimen (B18021) of probable late Viséan age from Visé, Belgium.

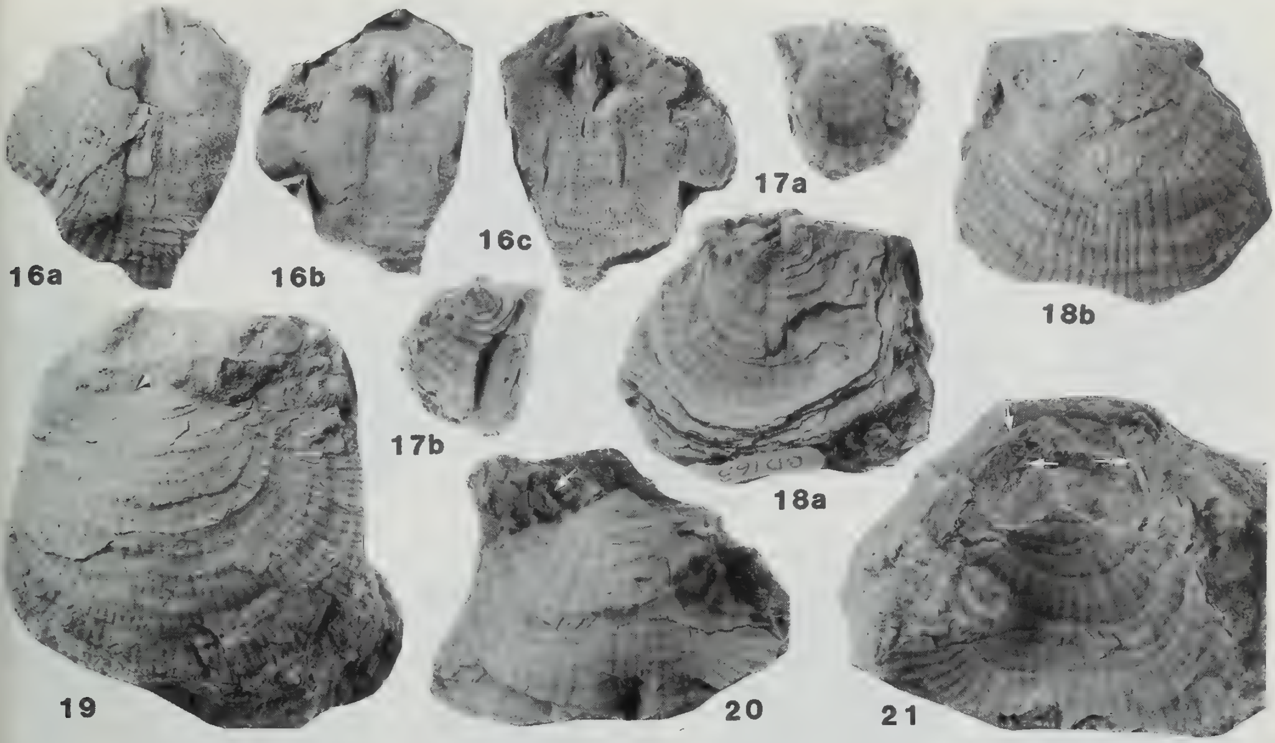
AGE. Late Asbian, in Britain, to early Namurian in the CIS (former USSR).

DESCRIPTION. The outline is subcircular, but retaining a straight hinge line with a maximum width of about 50 mm; it varied somewhat, depending on the degree of growth distortion. The ventral valve umbo may or may not extend beyond the hinge line. The lateral profile is commonly planoconvex, but with a minimum of ventral convexity leading to a very shallow body cavity. The curved length hardly exceeds the straight length. Concentric irregular rugae associated with lamellae are prominent on both valves. Ribbing has flattened crests and widens anteriorly, with six or seven ribs per 5 mm width at 10 mm from the umbo. Spines are distributed in a pair of rows from the umbo at an angle of about 20° from the hinge, with a maximum of seven to eight on each side (Fig. 19), many of which probably acted as clasping spines. Some specimens have rare additional body spines.

Internally the ventral valve resembles a very flat and broad *A. margaritaceus*, with elongate, slightly raised adductor scars. The very small ventral umbonal cavity means that the cardinal process is sessile. An alveolus may be present in some specimens, but a low and short median septum only arises between the anterior parts of the slightly raised adductor scars, which are ornamented dendritically. Weakly impressed brachial areas are irregularly surrounded by ridges, most prominently in the median sectors (Figs 16b, c). The valve surface is endospinose except posteromedially, behind the adductor scars. The ventral valve is also endospinose.

DISCUSSION. It has been common practice in Russia to attribute this species to Rotaï, at various dates. The earliest published mention of the species is Rotaï 1939: 470 [466], but he provided no description or illustration. We thus consider the first valid description to be that of Gladchenko (1955), which she repeated with the same illustrations in 1960. The lectotype was selected from Donbass material by Aizenverg in 1983. The age of this specimen, according to Poletaev *et al.* (1991), is early E_2 (=Arnsbergian).

The large size, style and width of ribbing and spines on the body anteromedially, although irregularly present because of attachment to hard surfaces, help to place the species in *Argentiproductus*. The large size and very flat form of the shell, with hardly any inflation at the tip of the ventral umbo, distinguish it from other species of the genus. All external characteristics, including the degree of ventral convexity, are variable because of the conditions under which the species



Figs 16–21 *Argentiproductus atripoides* (Gladchenko). Figs 16a–c, the largely exfoliated body cavity region of a specimen showing the ventral muscle scars and the mould of the dorsal interior, with (Fig. 16c) a latex cast of the dorsal valve interior. Stebden Hill. BD1620. ×1. Figs 17a, b, ventral and dorsal views of a juvenile specimen showing the early development of dorsal lamellae. Stebden Hill. BD1632. ×2. Figs 18a, b, dorsal and ventral views of a specimen showing the strong dorsal lamellae. Stebden Hill. BD1631. ×1·5. Fig. 19, ventral valve exterior showing lamellose shell and spine rows. Glutton, Derbyshire. B53582. ×1. Fig. 20, a ventral valve exterior with the row of flank spines on the left side (arrow) extending into the rock. Stebden Hill. BD1616. ×1·5. Fig. 21, posterodorsal view of an incomplete specimen showing the flanking spines (arrows) curving in a clasping fashion posteroventrally. Stebden Hill. BD1611. ×1·5.

lived, *viz*. within framework facies of Cracoean reefs in which other organisms provided local hard surfaces for attachment (see Brunton & Mundy 1988*b*, Mundy 1978, 1980). The extent to which ventral valves adpressed to hard sufaces or grew against hard objects influenced greatly the shape of the valve and its ornamentation. In addition specimens seem to have been prone to damage so that some shells display large areas of shell regeneration (Figs 18a, b). These characteristics make the species appear similar to the oyster-like bivalve *Pachypteria,* with which it is found in reef frameworks. No umbones are sufficiently well preserved to display the expected juvenile pedicle sheath, but at least some of the more median umbonal flanking spines were curved posteromedially, as if acting as claspers (Fig. 21). We have seen no indication of a cicatrix.

We attribute the Craven specimens to this species because of their close similarity to the species as illustrated by Gladchenko (1960) and Galitskaya (1977) from the Protvinsky horizon (=early Arnsbergian, Lower Namurian) of central Tien Shan, Kirkizia. Unfortunately details of the lithology from which the Tien Shan specimens came are unknown. Although the rocks of the Tien Shan are correlated with the Arnsbergian, some other species found at the same horizon indicate to us a slightly older age, nearer the base of the Namurian. Nevertheless, if the Craven specimens are correctly assigned it means that the species has a stratigraphical range of at least Asbian to within the Pendleian and early Arnsbergian.

Genus *PRODUCTINA* Sutton, 1938

1938 *Productina* Sutton: 151.
1965 *Productina* Sutton; Muir-Wood: H471.
1967 *Productina* Sutton; Carter: 289.

TYPE SPECIES. *Productus sampsoni* Weller (1909: 300; pl. 12, figs 18–22), by original designation of Sutton, 1938.

DIAGNOSIS. Slightly elongate outline, with an inflated umbo; ribbing distinct and regular with rounded crests. Spines few at flanks and may be lacking medially.

DISCUSSION. *Productina* species differ from the late Devonian genus *Dorsirugatia* (Lazarev, 1992 & herein, p.117) in having a more inflated ventral umbo and well defined regular ribbing. *Productina* differs from *Argentiproductus* in being more elongate in outline, and more globose in profile (i.e. with an inflated ventral umbo), with a less lamellose ventral valve (retaining a strongly lamellose dorsal valve); in consequence the ribbing is more regular. The ribs are rounded in section and, while they widen anteriorly, this feature is less marked than in *Argentiproductus*. The posterolateral spine patterns are similar in both genera, but *Productina* tends to lack or to have very few median spines. A feature common to both genera is the tendency for rib branching to occur in association with lamellae. In the more strongly ventrally lamellose *Argentiproductus* species this results in a varied ribbing, both in terms of rib width and degree of development of the ribs. Quite commonly, immediately anterior to a lamella the ribbing diminishes or reverts to a low single rib where posteriorly it had divided. On the less lamellose *Productina* species the ribbing is more continuous, less varied in dimensions and each rib has a more rounded crest.

Internally the two genera are more similar than indicated by Muir-Wood & Cooper (1960: 182) because of their use of a misidentified dorsal interior (1960: pl. 123, fig. 17), belonging perhaps to a linoproductid species. However, even with incomplete knowledge of interiors of all species, it seems that some congeneric species display as much variation as is seen between the two type species.

Sutton's genus is based on *P. sampsoni* from the Chouteau Limestone of Missouri, of upper Kinderhookian age (= Hastarian, Lower Tournaisian). In North America *P. parvula* (Winchell, 1863), from similarly aged rocks in Iowa, and possibly *P. lodgepolensis* Rodriguez & Gutschick (1968), from mid Tournaisian rocks of Montana, belong to this genus. Roberts (1963, 1976) described several Tournaisian to Viséan species from Australia, but following Brunton (1966) assigned them to *Productina*. We assign his *P. macdonaldi* to *Argentiproductus* but keep his *P. globosa*, of late Tournaisian age, and *P. striata*, of mid Viséan age, in *Productina*. Of Paeckelmann's (1931) two species from Germany, *P. decheni* of Tournaisian age probably belongs here, but *P. transverisstriatus* cannot be assigned with confidence. In Britain we assign *P. pectinoides* Phillips (1836) to *Productina* and compare some species from the Craven Reef Belt to the species. Winkler Prins (1968) and Martinez Chacon (1979) recorded poorly preserved material as *P. pectinoides* from early Bashkerian strata. The genus, therefore, extends from the early Tournaisian to rocks of early Bashkerian age.

Productina pectinoides (Phillips, 1836) Figs 22, 23

1836 *Producta pectinoides* Phillips: 215; pl. 7, fig. 11?
?1931 *Productus (Thomasina) pectinoides* (Phillips); Paeckelmann: 188; pl. 17, figs 13, ?14–16.
?1968 *Productina pectinoides* (Phillips); Winkler Prins: 75; pl. 1, figs 13, 14.
?1979 *Productina pectinoides* (Phillips); Martinez Chacon: 132; pl. 12, figs 14–23.
1985 *Productina pectinoides* (Phillips); Zakowa: 308; pl. 3, figs 1–6.

DIAGNOSIS. Large for genus, reaching about 30 mm wide, with small ears almost forming maximum shell width. Ventral valve with weak lamellae; ribs regular, with rounded crests, approximately 10 per 5 mm width at 10 mm from umbo.

TYPE SPECIMEN. Lectotype, here chosen, BMNH B8947 (Figs 22a–c) in the Gilbertson Collection and figured by Phillips (1836: pl. 7, fig. 11). The locality is given as 'Bolland'.

MATERIAL. A second smaller specimen (paralectotype) in the Gilbertson Collection, BMNH BB65110; about 12 other NHM specimens including material from the reefal facies at Narrowdale (e.g. B48709–18), Staffordshire. One specimen from Kendal, Cumbria, in the Sedgwick Museum, Cambridge (E9710).

AGE. Chadian to Asbian, and possibly Brigantian.

DISCUSSION. It is a common feature of specimens described by Phillips that details of their localities are unknown. Thus this species is recorded as 'Bolland', a region extending northeast of Preston and to the northwest of Clitheroe, roughly centred on the river Hodder and now forming part of the area known as the Forest of Bowland, Lancashire. Thus precise localities and ages remain unknown. However, it seems that true examples of the species occur in the Clitheroe area in Chadian rocks belonging to the Clitheroe Limestone Formation of Riley (1990*b*), who demonstrated that the Chadian in this area lies within the late Tournaisian. The Phillips specimens could also be of this age.

Productina specimens from the Craven faunas were initially identified by us as *P. praemargaritaceus* (Sergunkova), and this name was used by Brunton & Tilsley (1991) for some specimens from Treak Cliff, Derbyshire. *P. praemargaritaceus* is a Russian Tournaisian species and we now recognize that it differs from the Craven Reef Belt specimens, and others identified here as *P. pectinoides,* by being wider and less globose, so we assign it to *Argentiproductus*. The Treak Cliff specimens referred to above should be called *P.* cf. *pectinoides*. The Craven Reef Belt specimens collected by Mundy are rare and not all are well preserved. While one is a good match to the small Gilbertson specimen of *P. pectinoides* the others belong less clearly to the species. Thus in order to retain a clear diagnosis of *P. pectinoides* we separate the Craven specimens below as *P.* cf. *pectinoides*.

The large forms of *A. margaritaceus* somewhat resemble large examples of *P. pectinoides,* but the ribbing, ventral lamellae and more spinose *Argentiproductus* species distinguish them. *P. pectinoides* has a more strongly inflated umbonal region than *Argentiproductus* species and its more evenly ribbed and less lamellose shell produces a more regular appearance. In addition, in this species the angle at which spines diverge from the hinge line is less, at about 10°, than the *c.* 15°–20° in *Argentiproductus*.

The species name has not been used much in European literature. Those specimens described by Paeckelmann (1931), Winkler Prins (1968) and Martinez Chacon (1979) may not be entirely conspecific, while the late Asbian and Brigantian record of Zakowa (1985) looks accurate.

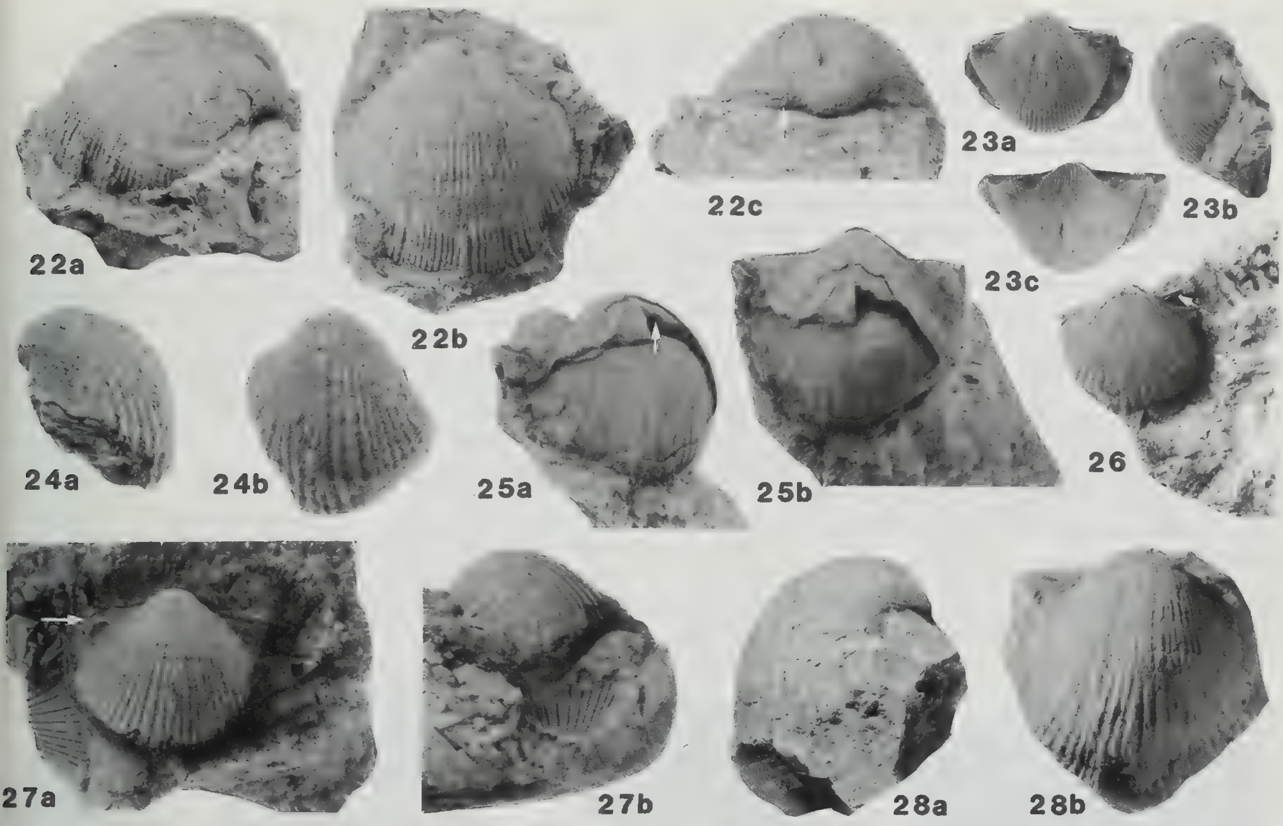
Productina* cf. *pectinoides (Phillips, 1836) Figs 24–28

MATERIAL. Twelve specimens in the DJCM collection largely from Butter Haw Hill, and a single specimen from the same locality in the Liverpool Museum.

AGE. Asbian.

DISCUSSION. We compare this material to *P. pectinoides* since its preservation is imperfect and we cannot be fully confident that it is conspecific with Phillips' species. These specimens are found contemporaneously with *A. margaritaceus* in the Craven Reef Belt, but differ by the generic characters already discussed. The specimens are all small, reaching a maximum width, just anterior of the ears, of 14 mm. While they resemble the lectotype of the species in most aspects, the degree of umbonal convexity (inflation) is slightly less and three specimens have ribs which anteriorly became wider, and thus resemble *A. margaritaceus*. We have separated the Craven specimens here from the true *pectinoides* so as to present a 'clean' diagnosis of the species.

In the final section of this paper (p.116) we discuss the stratigraphical relationships of this species with others of the subfamily.



Figs 22–23 *Productina pectinoides* (Phillips), from the Gilbertson Collection, figured by Phillips (1836), Bolland, Lancashire. Figs 22a–c, the **lectotype** (here selected), viewed laterally, ventrally and posteriorly. B8947. ×1. Figs 23a–c, the second small specimen (paralectotype) in the Gilbertson Collection, viewed ventrally, laterally and posteriorly. BB65110. ×1.

Figs 24–28 *Productina* cf. *pectinoides* (Phillips). Figs 24a, b, a small specimen in lateral and ventral views. Skelterton Hill. BD1674. ×2. Figs 25a, b, oblique anterolateral and ventral views of an incomplete specimen, showing the shallow body cavity (arrowed). Butter Haw Hill. BD1667. ×2. Fig. 26, a ventral view, showing one spine (arrowed). Butter Haw Hill. BD1668. ×1·5. Figs 27a, b, ventral and lateral views of a specimen with one pair of flank spines (arrowed) near the ears. Butter Haw Hill. BD1666. ×2. Figs 28a, b, lateral and ventral views of a large specimen from the Kendal area, Cumbria, closely resembling the type specimen. Sedgwick Museum, Cambridge, E9710. ×1.

Family **PLICATIFERIDAE** Muir-Wood & Cooper, 1960

Diagnosis emended. Small to medium productoids in which the ventral visceral disc is only gently convex, giving a shallow to moderate body cavity. Concentric ornament is strong, the ribbing weak to lacking. Spines commonly confined to ventral valves. Internal dorsal marginal structures are usual.

Subfamily **PLICATIFERINAE** Muir-Wood & Cooper, 1960

Diagnosis emended. Plicatiferids with moderately deep body cavities, strongly rugose or lamellose visceral discs and dorsal ear baffles.

Discussion. These familial diagnoses differ from those given in 1960 or the *Treatise* (1965) as they are new working diagnoses for the revision of the brachiopod *Treatise* now in progress. Muir-Wood & Cooper's (1960) subfamily included only *Plicatifera*. The newly evolving classification elevates the taxon to family level with the inclusion of several subfamilies and many more genera.

The Plicatiferidae includes genera from late Devonian to early Permian, while the subfamily is confined to Viséan and Namuriam rocks, the genera from western Europe being *Plicatifera, Aseptella* Martinez Chacon & Winkler Prins (Namurian of north Spain) and the new genus *Admodorugosus* described herein (p.111).

Genus ***PLICATIFERA*** Chao, 1927

1927 *Plicatifera* Chao: 25
1960 *Plicatifera* Chao; Muir-Wood & Cooper: 201
1965 *Plicatifera* Chao; Muir-Wood: H476
1966 *Plicatifera* Chao; Brunton: 203

Type species. *Productus plicatilis* J. de C. Sowerby, 1824, by original designation of Chao, 1927.

Diagnosis. Plicatiferinae with strong posterior rugae and variably developed ribbing, producing posterior reticulation in some species. Trails are smooth or faintly ribbed. Few spines are confined to ventral valves. The body cavity becomes deep anteriorly and ear baffles are prominent.

Discussion. *Plicatifera* is a characteristic and well-recognized genus in the Upper Viséan of Europe and parts of Asia. In profile the rugose visceral regions are rather flat, with the strongest convexity occurring with the anteriormost rugae and start of the trail, which can be long. The dorsal valve of adult shells curves strongly (geniculates) against the ventral valve trail. Brunton (1966) commented upon the considerable size differences amongst specimens in the Sowerby type collection and suggested that further work might show that the larger forms should be named differently. Initially our study of specimens, showing similar size variation, inclined us to separate as new species the specimens about twice the size of those more commonly found, including the type specimens of both *P. plicatilis* and *P. pseudoplicatilis* Muir-Wood. However, as more specimens were studied the separation of these two groups narrowed and work first carried out by Timms (1978) indicated that these variations might be growth phenomena. Timms & Brunton (1991) pursued the idea and demonstrated that possibly *Plicatifera* specimens reached varied sizes by the time they geniculated, according to whether they grew rapidly or relatively slowly, and the length of time over which they grew before the geniculation event, which they equated with sexual maturity.

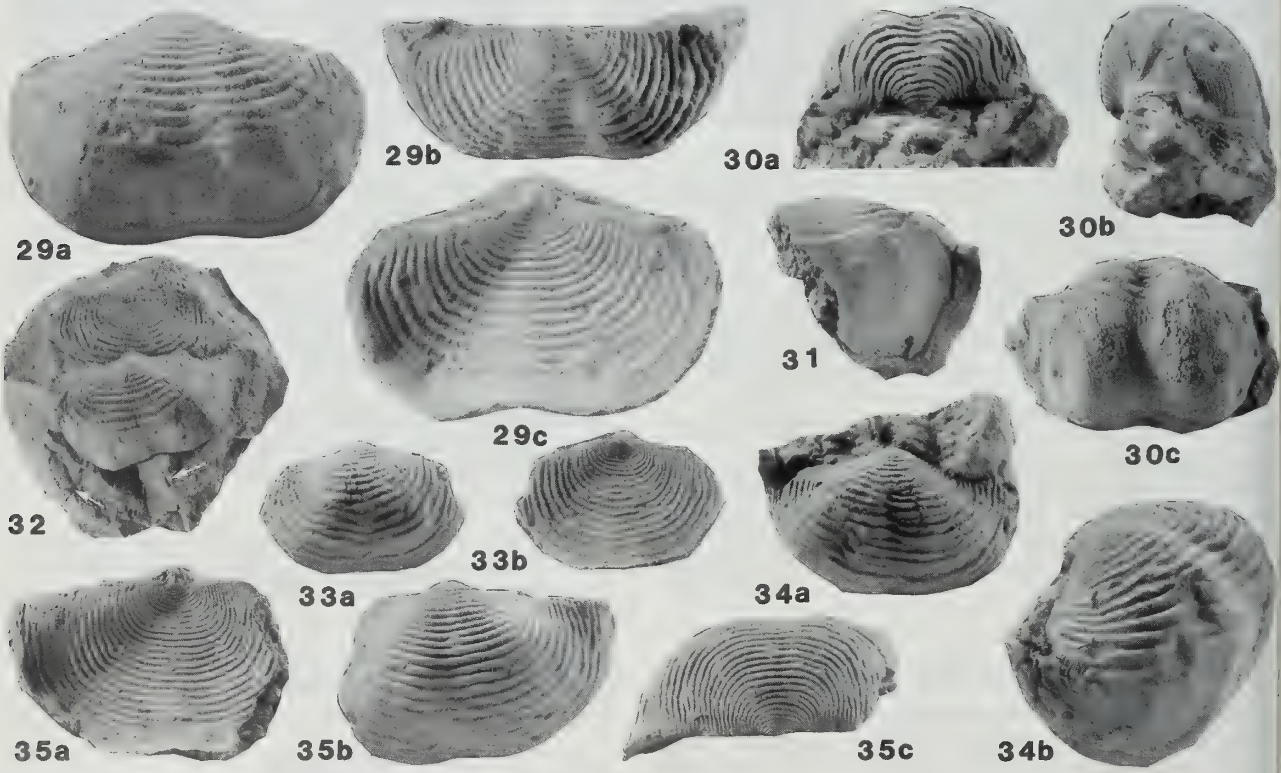
Plicatifera plicatilis (J. de C. Sowerby, 1824)

Figs 29–35

1824 *Producta plicatilis* J. de C. Sowerby: 85; pl. 459, fig. 2.
1914 *Pustula plicatilis* (J. de C. Sowerby); Thomas: 331; pl. 20, fig. 22.
1927 *Plicatifera plicatilis* (J. de C. Sowerby); Chao: 25.
1930 *Plicatifera plicatilis* (J. de C. Sowerby); Muir-Wood: 107.
1960 *Plicatifera plicatilis* (J. de C. Sowerby); Muir-Wood & Cooper: 201; pl. 56, figs 13–21 (?*non* figs 22, 23).
1965 *Plicatifera plicatilis* (J. de C. Sowerby); Muir-Wood: H477.
non 1966 *Plicatifera plicatilis* (J. de C. Sowerby); Brunton: 204; pl. 6, figs 6–15; pl. 7, figs 1–18.
1985 *Plicatifera plicatilis* (J. de C. Sowerby); Zakowa: 304; pl. 1, figs 5–7, pl. 2. figs 1–3.

DIAGNOSIS. *Plicatifera* lacking ribbing on visceral discs and trails.

TYPE SPECIMEN. Lectotype, BMNH B60960 (Figs 29a–c), designated by Thomas (1914: 331) when numbered 43392, from the Sowerby Collection. Locality unknown, other than Derbyshire.



Figs 29–35 *Plicatifera plicatilis* (J. de C. Sowerby). Figs 29a–c, the lectotype viewed anteroventrally, posteriorly and dorsally. Derbyshire. B60960. ×2. Figs 30a–c, posterior, lateral and anterior views of a specimen showing the smooth trail, spine bases and well developed median ventral sulcus. Elbolton. BD1602. ×1·5. Fig. 31, an incomplete specimen viewed anteriorly showing the gentle convexity of the visceral disc and smooth trail. Stebden Hill. BD1569. ×1·5. Fig. 32, a dorsal and a ventral valve, the latter showing two major spines from the anterior (arrowed). Derbyshire. B2471. ×1. Figs 33a, b, ventral and dorsal views of a specimen lacking its ears and most of the trail. Stebden Hill. BD1604. ×1. Figs 34a, b, a large example viewed ventrally (×1) and ventrolaterally (×1·5), showing some of the spine bases. Elbolton. BD1597. Figs 35a–c, dorsal, ventral and posterior views of one of the two larger specimens from the Sowerby Collection. Ventral spine bases and corresponding dorsal dimples can be seen. Derbyshire. B60962. ×1.

MATERIAL. Two other large specimens from the Sowerby Collection and numerous other specimens in the NHM; the DJCM collection contains 112 specimens in the NHM, from Stebden Hill and Elbolton, while 21 specimens from the same area are in the Liverpool Museum collections. Other specimens at the British Geological Survey, Keyworth, from Derbyshire and Yorkshire; the Sedgwick Museum, Cambridge, from Settle, Yorkshire; and in the Sheffield City Museum from near the Derbyshire/Staffordshire borders.

AGE. The Mundy collection specimens are all of Asbian, B_2 age, and the localities of other specimens, where sufficiently well known, indicate an Asbian age, late Viséan.

DISCUSSION. Two similar species of *Plicatifera* occur in the British Asbian, the type species and *P. pseudoplicatilis* Muir-Wood, 1928, described below. In 1966 Brunton incorrectly thought that the two were conspecific, so his very full description of '*P. plicatilis*' turns out to be what we would now call *P. pseudoplicatilis,* principally recognized by its ribbing and consequently reticulate visceral areas. Interiors of the two species seem to be very similar.

A variable feature of the Craven Reef Belt collections, but seen also in specimens from elsewhere, is a sulcation of the ventral valve which causes a posterior flexure in the anterior outline of the rugose area medially (Figs 30a, 32). Out of 46 well-preserved specimens of *Plicatifera plicatilis* in the NHM and Liverpool collections, 27 (59%) are sulcate; out of 44 good specimens of *P. pseudoplicatilis* 9 (20%) are sulcate. It is notewothy that the non-sulcate specimens almost always include the rare large examples referred to above. The curved lengths measured to the last ruga of geniculated specimens range from *c.* 12 mm to *c.* 35 mm. The body width (i.e. maximum width other than at the ears) is about 25 mm in the normal-sized specimens and about 44 mm in the large specimens.

Plicatifera pseudoplicatilis (Muir-Wood, 1928) Figs 36–46

1928 *Productus pseudoplicatilis* Muir-Wood: 189; pl. 11, figs 17a–c.
1930 *Eomarginifera pseudoplicatilis* (Muir-Wood); Muir-Wood: 204.
1966 *Plicatifera plicatilis* (J. de C. Sowerby); Brunton: 203; pl. 6, figs 6–15; pl. 7, figs 1–8.

DIAGNOSIS. *Plicatifera* with ribbing starting close to umbones and extending onto trails. Visceral discs are reticulate, but commonly non-sulcate.

TYPE SPECIMEN. Holotype, BMNH B20540 (Figs 36a–c) from Settle, Yorkshire (Muir-Wood 1928: 190).

MATERIAL. The NHM collections include 43 good specimens in the DJCM collection from Butter Haw and Stebden hills, and 11 more from the same localities are in the Liverpool Museum; there are several of the normal-sized specimens and one large specimen in the Sheffield City Museum.

AGE. Specimens from the Craven Reef Belt are all Asbian, B_2, and no other studied specimen contradicts this age.

DISCUSSION. The species was fully described from finely silicified material by Brunton (1966) (Figs 43–46), but then named *plicatilis.* The species is closely similar to *plicatilis,* differing mainly in that after a length of about 5 mm ribs started to grow which persisted until well beyond the last ruga and onto the trail (Fig. 39). This produced a reticulation on both valves in the rugose regions, but the rugae always predominate. Another difference is the dominance in *pseudoplicatilis* of non-sulcate specimens, which thus have a more regularly rounded anterior outline to the visceral region (Figs 36c, 40b).

As in *P. plicatilis* this species also has a rare large form, figured here from the reef facies of Narrowdale, Staffordshire (Figs 42a–d). Dimensions of the normal small and large forms of *pseudoplicatilis* specimens are a few mm less than those of *plicatilis.*

Subfamily LEVITUSIINAE Muir-Wood & Cooper, 1960

DIAGNOSIS, EMENDED. Plicatiferids with long trails and moderate to deep body cavities. Ribbing is lacking; rugae may be weak and marginal structures are lacking.

Genus *ACANTHOPLECTA* Muir-Wood & Cooper, 1960.

TYPE SPECIES. *Producta mesoloba* Phillips (1836: 215; pl. 7, figs 12, 13) by original designation of Muir-Wood & Cooper (1960).

DIAGNOSIS. Moderate sized shells with weak irregular rugae posteriorly. A median dorsal narrow sulcus and ventral fold bearing spines extends from disc to trail, the latter having small marginal flares or gutters.

COMMENT. The genus has been recorded in North America, north Africa, western Europe, Poland and Russia. It is not recorded with any confidence from the eastern C.I.S., China or Australia.

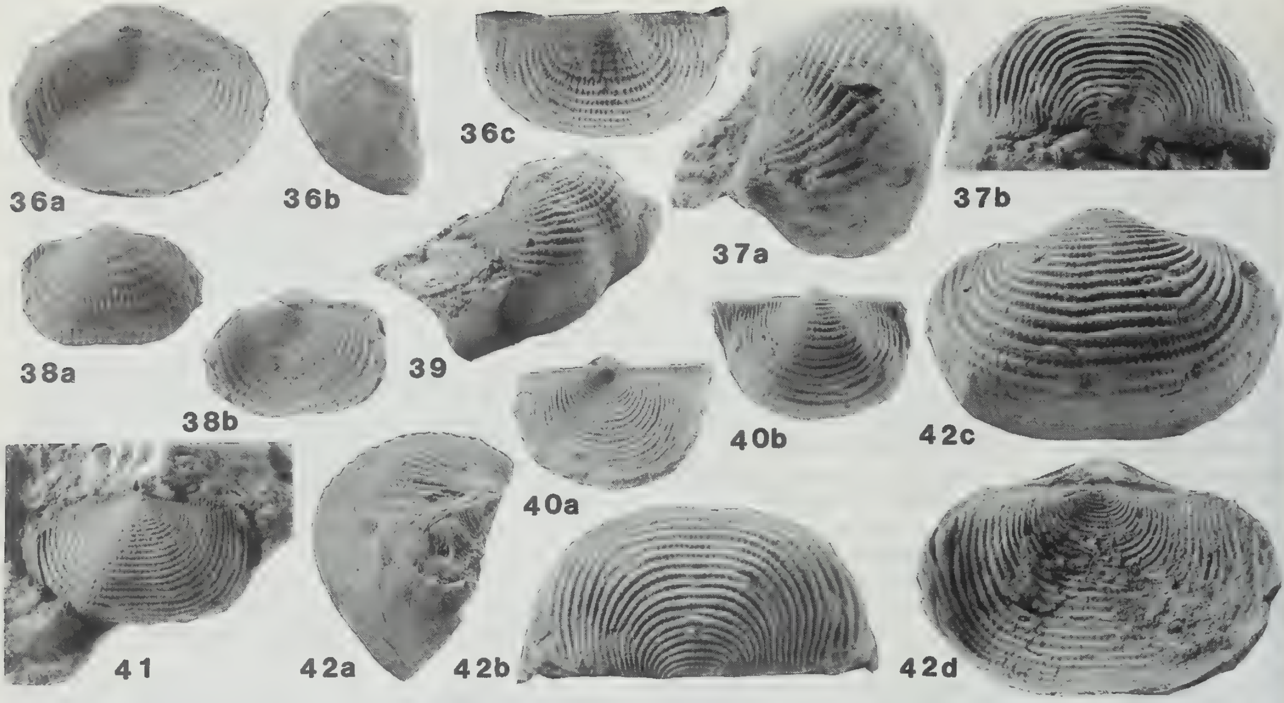
Acanthoplecta mesoloba (Phillips, 1836) Figs 47–53

1836 *Producta mesoloba* Phillips: 215; pl. 7, figs 12, 13.
1861 *Productus mesolobus* (Phillips); Davidson: 178; pl. 31, figs 6–9.
1914 *Pustula mesoloba* (Phillips); Thomas: 327; pl. 20, figs 18–21.
1930 *Plicatifera mesoloba* (Phillips); Muir-Wood: 107.
1960 *Acanthoplecta mesoloba* (Phillips); Muir-Wood & Cooper: 171; pl. 44, figs 10–17.
1966 *Acanthoplecta mesoloba* (Phillips); Brunton: 201; pl. 5, figs 16–22; pl. 6, figs 1–5.

DIAGNOSIS. Strongly and evenly concavoconvex in profile, with moderate body cavity. Ventral median fold in shallow sulcus, with spines, corresponding to dorsal weak sulcus. Adult trails with narrow anterolateral gutters.

TYPE SPECIMEN. Lectotype here chosen, Phillips' specimen figured on his plate 7, figure 12, BMNH B427, from Bolland (Figs 52a–b). Thomas (1914) misleadingly reported the types as lost, but the original specimens for Phillips' figures 12 and 13 are preserved in the Gilbertson Collection, used extensively by Phillips for his illustrations in 1836. The lectotype retains the original Gilbertson register number 160, proving that it came from the Bolland area rather than Derbyshire, the second locality mentioned by Phillips (1836: 215).

MATERIAL. Of the DJCM collections there are 33 specimens in the Liverpool Museum and 27 in the NHM. The latter



Figs 36–42 *Plicatifera pseudoplicatilis* (Muir-Wood). Figs 36a–c, the holotype of Muir-Wood (1928) in dorsal, lateral and posterior views. The shell material is partially missing, especially from the ventral valve, so that ribbing is less distinct. Settle, Yorkshire. B20540. ×1·5. Figs 37a, b, ventrolateral and posterior views of a slightly exfoliated specimen. Stoney Middleton, Derbyshire. Sheffield City Museum H88–196. ×1·5. Figs 38a, b, ventral and dorsal views. Stebden Hill. BD1565. ×1·5. Fig. 39, anterolateral view of a specimen showing the ribbing on the trail. Butter Haw Hill. BD1553. ×1·5. Figs 40a, b, dorsal and ventral views of an incomplete specimen. Butter Haw Hill. BD1584. ×1·5. Fig. 41, an exfoliated dorsal valve interior. Stebden Hill. BD1562. ×1·5. Figs 42a–d, lateral, posterior, ventral and dorsal views of a large specimen showing the ribbing extending onto the trail and spine bases on the ventral and lateral surfaces. Narrowdale, Staffordshire. B45692. ×1·5.

collections also contain about 40 other specimens from Staffordshire, Derbyshire, Yorkshire, Ireland, North Wales, the Midland Valley of Scotland, and the Isle of Man. There are a few specimens, some cited by Thomas (1914), in the British Geological Survey collections and about 15, mostly from Derbyshire, in the Sheffield City Museum.

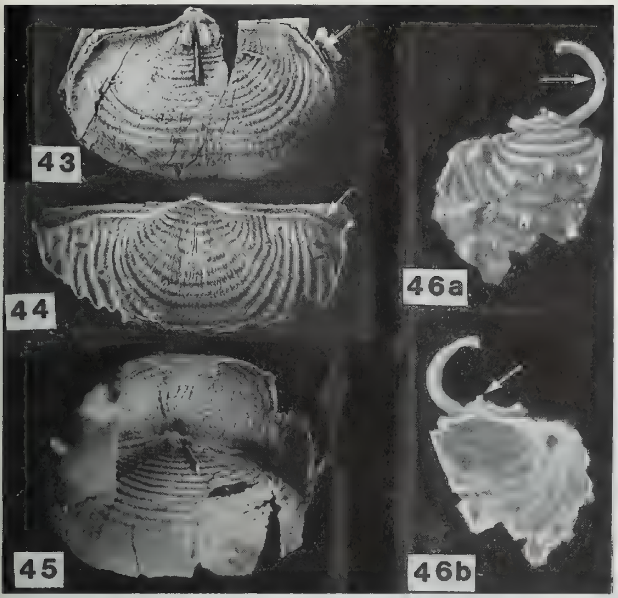
AGE. Most of the above specimens are thought to be of upper Viséan, Asbian to early Brigantian age. However, there are a few specimens named *A. mesoloba* in the NHM collections from Thorpe Cloud, Derbyshire, generally considered as of Chadian age, and Thomas (1914) referred to a specimen which may be of Arundian age. The species has been recorded from Brigantian (P_2) reef facies of the Eyam Limestone Formation near Monyash, Derbyshire by Gutteridge (1990). We thus attribute an age of Chadian to Brigantian for the species. The relationship of these Chadian rocks to the Tournaisian/Viséan boundary in this area is unclear.

DISCUSSION. While the species occurs most commonly during Asbian times it also occurs in Chadian and Brigantian reef facies. The Chadian records from Thorpe Cloud are specimens possibly displaying some differences as compared to the types, such as a more regular rugation and less well defined median fold and sulcus; the spine bases also seem less prominent. In the Sedgwick Museum, Cambridge, there are four (E9745–48) small specimens from County Clare, Ireland, only about 18 mm wide and somewhat resembling the Thorpe Cloud material; these may also therefore be early Viséan in age.

The NHM specimens, including those from the Craven Reef Belt, display a range in adult size comparable to the range discussed above for *Plicatifera*. There is also variation in the strength of development of the median sulcus within which lies the narrow ventral fold. Commonly these structures make little difference to the general anterior outline, but in some specimens the depth of the sulcus causes an emargination anteriorly. Again this feature is comparable to the more sulcate forms of *P. plicatilis*.

The species is a rare constituent of the fauna from County Fermanagh described by Brunton (1966), but a full description was given, including illustrations of the dorsal valve gutter bordering the trail (Figs 49a–c). This stucture tends to have been lost from specimens cracked out from the rock, but the lectotype, and a few others, show the start of the outward curve of the trail (Fig. 52a) which, if complete, would have been the gutter.

The species differs from *Plicatifera* in being more regularly convex, with no true geniculation in either valve. This convexity of the dorsal valve produced a body cavity shallower than in adult *Plicatifera*, and the outline is also more rounded. The low irregular rugae, double row of spines close to the hinge line and median fold and sulcus further distinguish this species from *Plicatifera*. *A. mesoloba* differs from *Admodorugosus* (below) by being at least twice as wide across the body, in its non-rugose and guttered trail, and median fold and sulcus.



Figs 43–46 *Plicatifera pseudoplicatilis* (Muir-Wood). Four silicified specimens from the Asbian of Co. Fermanagh, Ireland. Fig. 43, a dorsal valve interior showing the lateral ridges and ear baffles (arrowed), adductor scars and faint brachial ridges. BB52835. ×1·7. Fig. 44, an incomplete ventral valve interior showing lateral ridges (arrowed), adductor and diductor muscle fields. BB52834. ×2. Fig. 45, incomplete articulated dorsal and ventral valves showing the deep adult body cavity and the way in which the lateral ridges fit together. BB52837. ×1·7. Figs 46a, b, a juvenile ventral valve viewed externally and internally, showing the initial clasping spines (arrowed), other juvenile spines and the pedicle sheath (arrowed). BB52840. ×10.

A. mesoloba occurs in western Europe, Poland and Russia (Moscow basin).

Genus *ADMODORUGOSUS* nov.

Diagnosis. Small to medium sized plicatiferinid with prominent concentric rugation covering both valves, but lacking radial ornament. Few scattered spines are confined to ventral valves. Body cavity is moderately shallow.

Name. Latin, *admodum* = entirely, *rugosus* = wrinkled.

Type species. *Admodorugosus cracoensis* nov.

Discussion. Only the type species is recognized, and it is described below.

Admodorugosus has been confused in the past most commonly with *Acanthoplecta* Muir-Wood & Cooper or *Plicatifera* Chao. When complete specimens are available those genera are differentiated by their smooth trails, the posterior ribbing of some *Plicatifera* species and the median spine-bearing ridge, within a sulcus, on *Acanthoplecta*. If only the posterior, visceral regions are available identification is less easy, but *Admodorugosus* is more rounded in both profile and outline than the other two genera. The rugation of the new genus is more comparable to that of *Plicatifera* than to that of *Acanthoplecta*, but adult *Plicatifera* specimens of the more common smaller dimensions may reach about twice the width of adult *A. cracoensis*, and their outlines are more quadrate. *P. pseudoplicatilis* (Muir-Wood) is also radially ornamented, producing a somewhat reticulate visceral region.

Other plicatiferid or leioproductid genera of different ages (and thus not expected in Viséan rocks) lack the clear rugation of *Admodorugosus*. The rugation on the Upper Devonian *Planoproductus* Stainbrook is weak and impersistent; in addition the ventral valve is covered by small spines. It should be classed with *Rugauris* Muir-Wood & Cooper in a separate family group. The leioproductid *Magnumbonella* Carter, from the Tournaisian of the U.S.A., has fine rugae posteriorly, but they do not extend onto the trails. Another rugose genus is *Acanthoproductus* Martynova from the late Famennian of Kazakhstan, but its rugae fail to extend onto the trail and posteriorly there are elongate spine bases which would seem to place the genus in the subfamily Semiproductinae McKellar 1970.

Admodorugosus cracoensis sp. nov. Figs 54–60

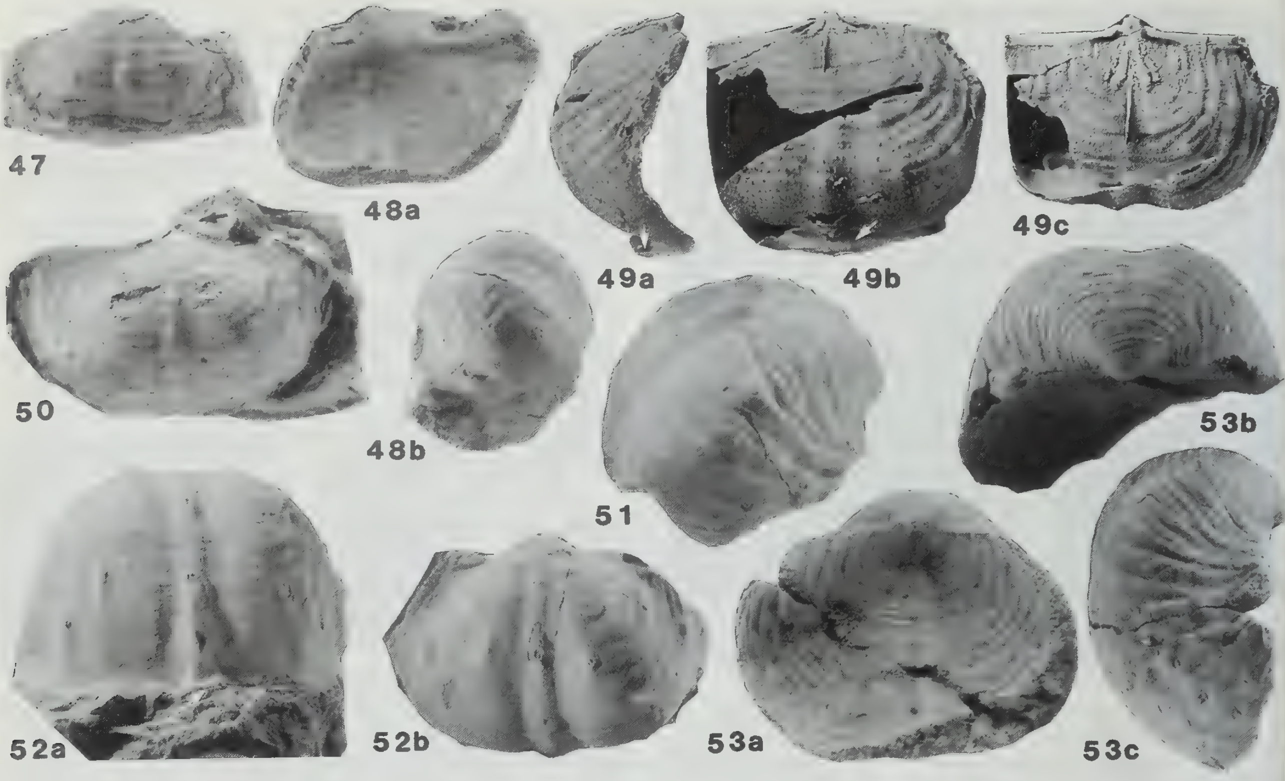
Name. The species is named after the village of Cracoe, North Yorkshire, which also gives its name to the tract of reef limestones from which many of the known specimens were collected.

Diagnosis. As for the genus.

Locality and horizon. The type locality is Butter Haw Hill (Grid Ref. SD 9964 6104), 11 miles (18 km) east of Settle, North Yorkshire, in late Asbian (B_{2b}), Dinantian reef limestones.

Holotype. Specimen in The Natural History Museum, London, BMNH, BD2447 (Figs 54a–d), from Butter Haw Hill, North Yorkshire, collected by DJCM.

Material. The 37 specimens (paratypes) examined in addition to the holotype are as follows: Eighteen specimens collected by DJCM from precise localities on Butter Haw Hill (BD2439–56, less BD2441–4,6), Skelterton Hill (BD2432–37), and Stebden Hill (BD2441–43), North Yorkshire. Five specimens from the 'Cracoe Reef Knolls' in the Garwood collection of the British Geological Survey, (67064–68); two Cracoe district specimens in the Liverpool Museum, (1976.249 Ex-Ey); two specimens from Treak Cliff, Castleton, Derbyshire, one in the Liverpool Museum collected by P.W. Phillips (1972.346.E), the other, collected by Dr P. Cossey, in the NHM (BD2446). Also in the Liverpool Museum are two possible specimens from Little Orme, north Wales. In the Sheffield City Museum there are four unnumbered Bateman collection specimens, possibly from Wetton, and one specimen (H88–244, called *mesolobus*) from Stoney Middleton, Derbyshire. The J.W. Jackson collection at Buxton contains a specimen (JWJ15112) from Peak Hill near Castleton and two from Narrowdale (JWJ15948). Other specimens, all in the NHM, are six collected by Carrington, in the Davidson Collection, from Wetton, Staffordshire (B5784, BD3206, BD3347–50); one Davidson Collection specimen from Narrowdale, Staffordshire (B13811); three specimens collected by Wheelton Hind from Narrowdale (B53674, B53677); three specimens in the Gilbertson Collection from Bolland (B429, B439, BD3202); one specimen collected by J.S. Turner from Little Island, Cork, Ireland (B95512); and one collected by P. Cambridge from Wirksworth Quarry, Derbyshire (BD6577).



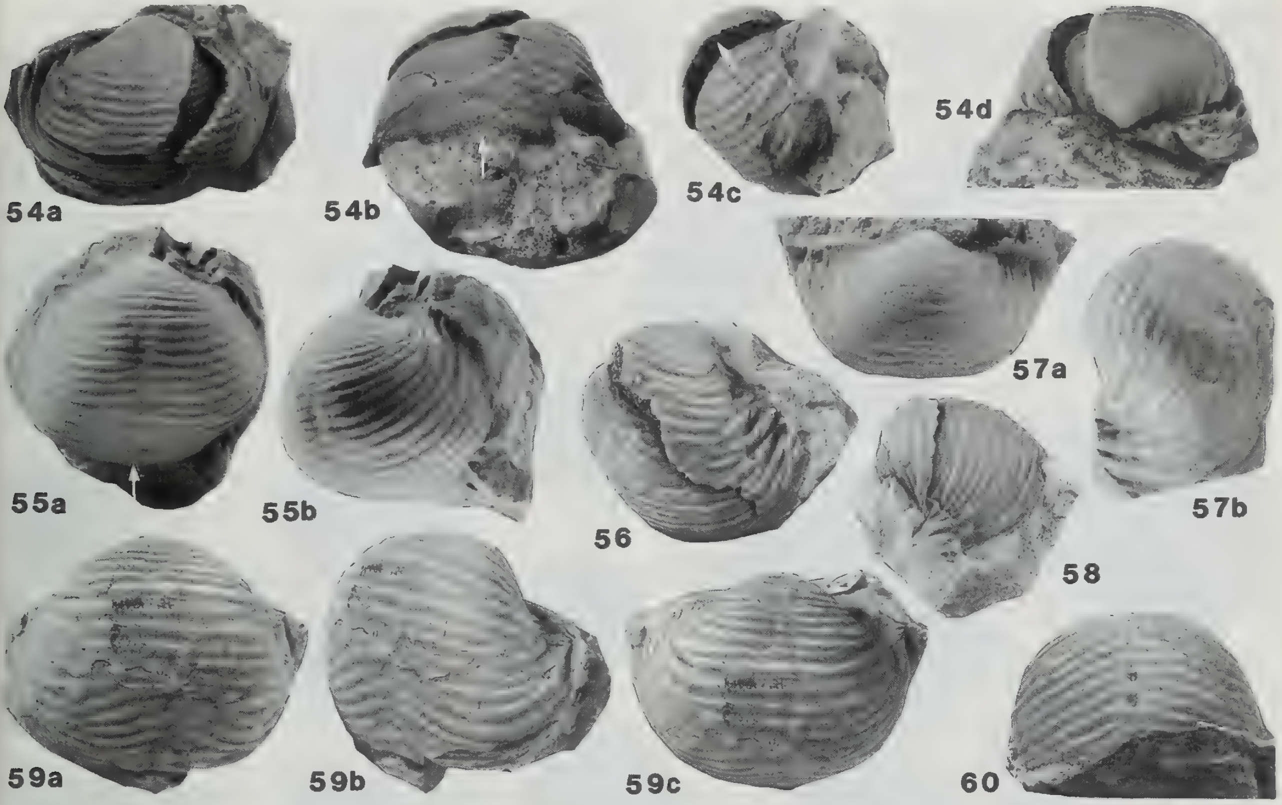
Figs 47–53 *Acanthoplecta mesoloba* (Phillips). Fig. 47, anterior view showing the slight outward turn of the valve margin indicating a gutter. Stebden Hill. BD1521. ×1. Figs 48a, b, dorsal and anterolateral views of a specimen showing the low median ridge within a shallow sulcus. Butter Haw Hill. BD1543. ×1·5. Figs 49a–c, a silicified dorsal valve from Co. Fermanagh viewed laterally and internally, showing the morphology and marginal gutter. BB52831. ×1·3. Fig. 50, an exfoliated dorsal valve interior showing the base of the cardinal process (arrowed) and parts of the gutter laterally. Stebden Hill. BD1531. ×1·5. Fig. 51, lateral view of a specimen from Bolland showing the spine bases on the flanks. BB61638. ×2. Figs 52a, b, **lectotype** (here selected), from the Gilbertson Collection, figured by Phillips (1836), viewed anteriorly and ventrally. The slight out-turn of shell at the ventral margin indicates a broken gutter. Bolland, Lancashire. B427. ×1·5. Figs 53a–c, dorsal, posterior and lateral views of an almost complete specimen showing flanking spine bases and dorsal valve dimples. Butter Haw Hill. BD1540. ×1·5.

AGE. All the Cracoe specimens collected by one of the authors (DJCM) came from late Asbian reef limestones containing goniatite assemblages indicative of B_{2b} zone age. None has been found in deposits of B_{2a} or P_{1a} age. It is considered likely that the four Cracoe specimens in the Garwood Collection of the British Geological Survey came from B_{2b} zone limestones. Eleven of the NHM specimens came from 'reefal' limestones of the Wetton and Narrowdale region of Staffordshire, or from Derbyshire, and are of the same age; two from Gilbertson's Bolland Collection could be of the same age, and the fourteenth is from J.S. Turner's Collection from the east side of Little Island, Cork, Ireland, where the rocks are also thought to be of late Asbian age. The Stoney Middleton specimen in the Sheffield City Museum is a possible exception, since rocks in the area could be Brigantian. However, as the specimen is so like all other Asbian specimens studied we conclude it also came from the Asbian rocks in the same region. It seems likely that *A. cracoensis* is confined to late Asbian reef limestone facies.

DESCRIPTION. Small (up to about 20 mm maximum width) thin-shelled plicatiferids with rounded, transversely oblong to depressed ovate, outlines when viewed dorsally. The lateral profile is strongly and evenly concavoconvex, but non-geniculate, and leaves a shallow body cavity. The ventral valve has a non-sulcate convex venter and trail, steep, slightly spreading flanks and reasonably well differentiated ears, which are flat and laterally tapering. The hinge line, including the ears, forms the widest part of the shell. The umbo projects only slightly beyond the hinge line. The dorsal valve closely follows the shape of the ventral valve, but the visceral area is flatter.

The ornamentation of both valves consists of distinct rounded rugae of consistent strength over the entire shell, other than the dorsal valve anteriorly where they are somewhat crowded and less well differentiated. Commonly there is a median deflection of the rugae posteriorly on the trail. Rugae increase, mainly on the flanks, by bifurcation and occasional intercalation; there are 6 or 7 rugae between 5 and 10 mm anteromedially from the ventral umbo. Spines are confined to the ventral valve, occurring on the crests of rugae and principally in two indistinct rows on the flanks and in a median row, associated with the flexure in the rugae on the trail. There are a few additional scattered spines. Growth lines are present on well-preserved valves.

Internal features are poorly known. In both valves there are weakly radial rows of tubercles and in ventral valves there



Figs 54–60 *Admodorugosus cracoensis* sp. nov. Figs 54a–d, **holotype** in ventral, anterior, lateral and posterior views. Note the shallow body cavity (arrowed), total rugation and median deflection of the ornamentation. Butter Haw Hill. BD2447. ×2. Figs 55a, b, ventral and ventrolateral views. Bolland, Lancashire. Gilbertson Collection, B439. ×2. Fig. 56, a specimen with its anterior ventral valve missing but showing some of the posterior spine bases. Wetton, Staffordshire. Davidson Collection, B5784/1. ×2. Figs 57a, b, ventral and anterolateral views of a specimen showing some delicate flanking spine bases. Wirksworth, Derbyshire. BD6577. ×2. Fig. 58, an incomplete specimen viewed laterally. ?Wetton, Staffordshire. Bateman collection (astutely labelled as 'undescribed'), Sheffield City Museum, [not numbered]. ×1·5. Figs 59a–c, anterior, anterolateral and ventral views of an almost complete specimen showing, despite a little shell damage, the characteristic deflection of rugae anteriorly. Wetton, Staffordshire. Davidson Collection, B5784/2. ×2. Fig. 60, an anterior view showing median spine bases. Wetton, Staffordshire. Davidson Collection, B5784/4. ×2.

are indications of a low ridge medially (e.g. B13811), separating the muscle fields. The dorsal valve has a low, sessile, strongly bilobed cardinal process (BD3350), as seen from the internal surface. There is a small alveolus and weak lateral ridges diverge slightly from the hinge line (e.g. BD2454, BD2456). There is no evidence of ear baffles.

Discussion. Although rather a rare species, it is distinctive and sufficient specimens have been accumulated to observe that in some the flanks are more widely spreading than in the other slightly narrower forms. Nearly half the specimens are somewhat exfoliated dorsal valves and, unless part of the ventral valve is also preserved, it is not always easy to recognize when the whole shell is not present. However, the lack of a projecting umbo, the relatively flat visceral disc and lack of any true spine bases should distinguish these dorsal valves.

Shape remained much the same during growth, between the observed widths of 12 mm to 21 mm, but, judging from growth lines, the ears became more prominent only during late stages of growth. Spines grew from the crests of rugae in a widely separated fashion, but there is a fairly distinctive median row of spines at about 4 mm intervals anteriorly and two rows each side extending anterolaterally from the umbo; one close to the hinge, at about 2 mm intervals, and the second following the curve of the flanks, at about 3 mm intervals. Clasping spines have not been seen but spines grew rarely at other positions on ventral valves only.

Admodorugosus cracoensis is typically levitusiinid in its rounded, strongly convex profile, rather shallow body cavity (Fig. 54c), median spines on a differentiated region of ventral valve ornament (the posterior deflection of the rugae), lack of any radial ribbing and lack of any dorsal ear baffles. Reasonably complete specimens cannot be confused with other contemporaneous species, but fragments resemble pieces of *Acanthoplecta mesoloba* (Phillips) or *Plicatifera plicatilis* (J. de C. Sowerby). The species, however, differs from *Levitusia* itself by being much smaller and in its fully rugose valves.

The complete covering of the shell by well differentiated rugae distinguishes *A. cracoensis* from other described *Acanthoplecta* or *Plicatifera* species; Carter's (1967) early Carboniferous *Acanthoplecta inopinata* from Texas, and *A. kirgisica* Galitzkaya 1977, from the early Viséan of Kurgisia, are both smooth trailed species.

The rugation is somewhat similar to that of *Fluctuaria* *undata* (Defrance), but this species is more elongate in outline than *A. cracoensis* and the valves are ornamented entirely by well developed ribs. The entire ribbing and more numerous ill-defined rugae of *Undaria manxensis* Muir-Wood & Cooper 1960 distinguish this species.

It is noteworthy that ten NHM unnamed specimens collected by J. Tilsley from Thorpe Cloud, of Chadian age, resemble *Admodorugosus* in size and general shape. They differ in their less clearly defined rugae, which may not extend fully onto the trail, and in seeming to have rather deeper body cavities. Their spine distributions are similar, including those anteromedially, but their spines are somewhat more prominent anteriorly. These specimens resemble, but are distinct from, the Tournaisian early *Levitusia* species *L. hyperborea,* which occurs in Russia.

DISTRIBUTION. The 38 recognized specimens all came from the British Isles; from Staffordshire, Derbyshire, North Yorkshire and southernmost Ireland. The species has been recognized neither from literature nor in collections from rocks of the same age in the Isle of Man, nor from Belgium, where it might be expected in reef limestones containing otherwise similar assemblages.

Genus ***GENICULIFERA*** Muir-Wood & Cooper, 1960.

1960 *Geniculifera* Muir-Wood & Cooper: 187; pl. 47, figs 11–15.

TYPE SPECIES. *Avonia boonensis* Branson (1938), by original designation.

DIAGNOSIS. Small subcircular in outline. Dorsal visceral disc is almost flat and the strongly convex ventral valve producéd a deep body cavity. Weak rugae occur posteriorly. No ribbing and sparse ventral spines.

DISCUSSION. The genus has not been described from the British Isles, other than the recent record from Treak Cliff, Derbyshire (Brunton & Tilsley 1991). Muir-Wood & Cooper (1960) included no species other than the type, which came from the Chouteau Limestone (early Mississippian = Tournaisian) of Missouri.

Geniculifera keyserlingiana (de Koninck, 1843)

Figs 61–71

1843 *Productus aculeatus* de Koninck (*non* Martin 1809 = Sowerby 1814): 200; pl. 10, fig. 8.
1847 *Productus keyserlingianus* de Koninck: 239; pl. 14, fig. 6.
1861 *Productus keyserlingianus* de Koninck; Davidson: 174; pl. 34, figs 15, 16.
1930 *Avonia keyserlingiana* (de Koninck); Muir-Wood: 106.

DIAGNOSIS. Ventral valve almost hemispherical in profile. Dorsal visceral disc about 10 mm wide, length shorter, almost flat and geniculate producing very deep body cavity and short trails. Slightly elongate swollen spine bases on ventral valve only, and long spines. No marginal structures and brachial impressions at 45° to hinge line.

TYPE SPECIMEN. Lectotype, here selected, specimen number R 50537(1) in the de Koninck collection, MNHN, Institut de Paléontologie, Paris (Figs 70a–c), from Visé, Belgium, probably of upper Viséan age.

MATERIAL. In the collections of the NHM there are about 40 specimens; most (23) come from Treak Cliff, Derbyshire. The DJCM collection contains 12 specimens, mainly from Elbolton, while 41 specimens from Stebden Hill are in the Liverpool Museum. There are two Davidson collection specimens in the NHM from the Settle area, significant through having been identified by de Koninck himself. In the Sheffield City Museum there are nine specimens, of which six are from Narrowdale. Settle material in the Burrows Collection, Sedgwick Museum, Cambridge, contains 21 specimens (E9618–39). The NHM collections from the Visé area of Belgium contain 17 specimens in the de Koninck collection, from where the species was first described, plus 7 others in old collections.

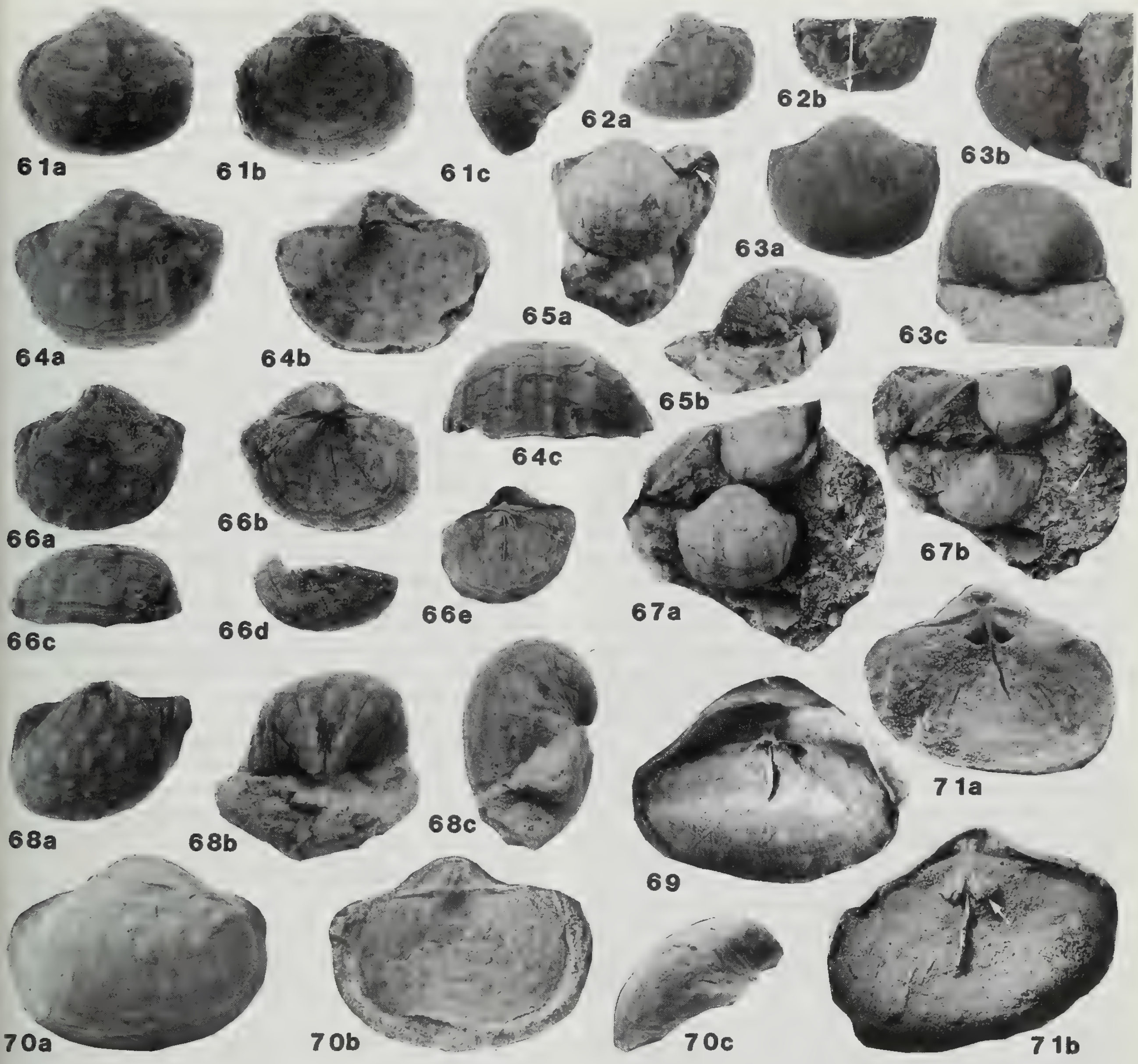
AGE. Upper Viséan, Asbian (B_{2a}, B_{2b}) and early Brigantian (P_{1a}).

DESCRIPTION. In outline the species is subrectangular, with the hinge line forming the widest part of the shell; the dorsal visceral disc is about 10 to 12 mm wide and 7 to 9 mm long. In profile the shell is almost planoconvex, the body part of the shell being almost hemisherical with simple trails reaching about 5 mm long. The umbo does not extend far beyond the hinge line and its flanks are not steep, so that the small ears are not strongly differentiated.

External ormanentation consists of relatively strong growth lines, weak irregular rugae posteriorly on most of the visceral region and spines on the ventral valve only, which arise from slightly elongate swollen spine bases. These are not necessarily associated with rugae, but tend to form a roughly quincuncial arragement with increasing separation anteriorly onto the trail. The spines are at high angles to the shell surface and may reach at least 7·5 mm long. Posteriorly, around the umbo, there are short, fine spines which appear to have been clasping. Dorsal valves have dimples, corresponding to the ventral spine positions, and geniculate quite strongly against the ventral valve. In a few large specimens a coarse costation developed along the trails.

Internally ventral valves have slightly raised elongate adductor scars reaching about 4·5 mm forwards from the umbo; the diductor scars spread fanwise anteriorly beyond the adductor scars. The swollen spine bases are visible internally and some of the flank and more anterior spines appear to have retained openings internally. Dorsal interiors have a sessile, separated, bilobed cardinal process, weakly supported laterally by slight cardinal ridges which do not extend into marginal structures. The adductor scars are well marked, commonly raised anteriorly and have triangular outlines. There is a weak median septum and brachial impressions extend from the adductor scars at about 45° anterolaterally. The internal surfaces of both valves have fine endospines.

DISCUSSION. De Koninck (1843) originally described the species as *P. aculeatus* Sow., but named it *keyserlingianus* in 1847. His descriptions and illustrations varied but significantly his earlier illustration (1843: pl. 10, fig. 8c) showed a section profile of the species displaying the very deep body cavity (see our Fig. 62b). Generally the 1847 illustrations are a little more accurate, but they give the false impression of a convex dorsal valve. Davidson's 1861 illustrations (pl. 34, figs



Figs 61–71 *Geniculifera keyserlingiana* (de Koninck). Figs 61a–c, ventral, dorsal and lateral views of a specimen figured by Davidson (1861: pl. 34, fig. 15). Settle, Yorkshire. Davidson Collection, B13818. ×2·5. Figs 62a, b, ventral and posterior views of an incomplete specimen showing the deep body cavity (arrowed). Elbolton. BD7563. ×1·5. Figs 63a–c, ventral, lateral and posterior views showing the high convexity of the ventral valve. Settle, Yorkshire. Davidson Collection, BB61545. ×2·5. Figs 64a–c, ventral, dorsal and anterior views of a specimen showing swollen spine bases and dorsal dimples. Skelterton Hill. BD7562. ×2·5. Figs 65a, b, ventral and lateral views of a specimen showing a spine extending into the rock (arrowed). Treak Cliff, Derbyshire. BD9332. ×1·5. Figs 66a–e, ventral, dorsal, anterior and lateral views of a partially exfoliated specimen (×2·5), and a latex cast taken from the dorsal interior (×2). Visé, Belgium. De Koninck Collection, B18242. Figs 67a, b, ventral view of a specimen on rock with a long spine (arrowed), and the same with the ventral valve removed showing a mould of the dorsal exterior. Treak Cliff, Derbyshire. BD9331. ×1·5. Figs 68a–c, ventral, posterior and lateral views of an internal mould showing swollen spine bases and raised ventral adductor muscle scars. Belgium. Natural History Museum (old collection) 97490. ×2·5. Fig. 69, latex cast taken from a specimen from Visé showing the dorsal interior in relation to the ventral umbo. Paris, R50537/2. ×3. Figs 70a–c, **lectotype** (here selected) in ventral, dorsal and lateral views. Note the flat dorsal valve and missing trail. The specimen has been slightly flattened. Visé, Belgium. Paris, R50537/.1. ×3. Figs 71a–b, dorsal view of an internal mould and a latex cast taken therefrom showing the raised adductor muscle scars (arrowed), cardinal process and brachial impressions. Visé, Belgium. Paris, R50537/3. ×3.

15, 16) of the species from Settle, Yorkshire, are good, although the dorsal internal mould illustrates brachial impressions in which the near horizontal component is over- accentuated (see our Figs 66e, 71a). In addition both de Koninck and Davidson rather over-stressed the swollen spine bases in their drawings. This feature is variable so their drawings are good for some specimens, but commonly the swellings are much less prominent.

In the NHM there are over 20 specimens labelled *P. keyserlingianus* de Koninck from the Visé area of Belgium, but they are not all conspecific, some being another deep-bodied species, *Institifera tessellata* (de Koninck). These specimens are said to have been from the de Koninck collection, but his material became so widely spread, some of it *via* dealers, that it is difficult to be sure of provenance. No specimen closely resembles any of de Koninck's figures, but one registered as NHM 97490 is a good internal mould of the ventral valve. As the substance of the shell was thin the external morphology is also reasonably displayed (Fig. 68a), showing how some spines retained internal openings, as well as the ventral muscle fields.

The species differs from *Quasiavonia aculeata* (J. de C. Sowerby) in its deeper body cavity resulting from its virtually flat dorsal valve, in its slightly rugose posterior and in not having the somewhat lamellose growth lines characteristic of *Q. aculeata.* Another deep-bodied and similar-sized species is *I. tessellata,* but this species has an elongate outline, and more or less continuous coarse costae between which are concentrically arranged dimples. In addition *Institifera* has dorsal trails which curve inwards over the dorsal valve and outwards from the ventral valve, forming a rolled structure marginally.

The young of *Acanthoplecta* and *Plicatifera* differ from *G. keyserlingiana* in being relatively wider, less convex ventrally, and in having rugae which are better developed. The regular ventral convexity, deep body and size resemble *Eomarginifera trispina,* but the lack of ribbing, poorly defined ears, numerous swollen spine bases and lack of internal marginal structures differentiate these species.

The type species of *Geniculifera, G. boonensis* (Branson, 1938) from Missouri, and another species *G. brevicula* Carter, 1967 from Texas, are late Tournaisian in age. These species differ from the British specimens in having rather flatter ventral valves so that the body cavity is slightly less deep and the valves bend rather more sharply between the visceral region and trails. The spine bases of the American species are less swollen and the frequency of spines greater in the Texas species. The assignment, therefore, of *keyserlingiana* to *Geniculifera* extends the range of that genus from the Tournaisian of North America to the upper Viséan of western Europe. At present the only other species known which is assigned to the genus from younger rocks is *G.* (?) *ukrainica* Aizenverg, 1983 from the Arnsbergian of the Ukraine.

PALAEOECOLOGY AND DISTRIBUTIONS

The species considered here, with the exception of *A. atripoides,* were free-living adults which lived epifaunally or quasi-infaunally, supported in the sediment by their shell surfaces and spines. In common probably with all other productidines, these species had an initial pediculate stage (a pedicle sheath has been described and figured on *Argentiproductus* and *Plicatifera* (Brunton 1965), but see also Figs 13a, b & Fig. 46b here), followed by clasping spines which augmented and secured the initial juvenile attachment; clasping spines have been observed on *Argentiproductus, Plicatifera, Acanthoplecta* and *Geniculifera.* With further growth, shells broke clear of their attachment surfaces and lived free on the substrate, stabilized and supported by various spine configurations. These adult free-living species occured in flank and bank facies within the Cracoean buildups with little or no obvious bathymetric selection between deeper or shallower water, but over a depth range of up to 120 m. Trivial numbers have, however, been located in the shallow water framework facies where they must have occupied sediment 'pools' within the framework.

Argentiproductus atripoides, in contrast, is unique to the framework facies (Table 1), occuring in significant numbers in this niche on the summit of Stebden Hill. Here the species formed part of a specialized shelly community which colonized the framework (stromatolite–sponge–bryozoan–coral framestone–bindstone), a community including shelly attached aulostegaceans (Mundy & Brunton 1985, Brunton & Mundy 1988*b*), chonopectinids (Brunton & Mundy 1986) and pseudomonotid 'oyster-like' bivalves. The adaptive strategy of *A. atripoides* was the continued growth of clasping spines (Fig. 21) beyond the juvenile stage, with the flank spine row (which typically is of ventrolateral support spines in free-living species) forming posteriorly directed attachment spines, somewhat suggestive of aulostegaceans. A further adaptation to the framework niche is the robust, thick shell with flattened profile, giving the species a superficial oyster-like form, a comparison which is all the more apparent when specimens occur directly with the pseudomonotids; this shell form would be well suited to the higher energy environment expected in this exposed niche. The species is also recorded from Glutton, Derbyshire, where similar patches of reef framework facies occur (Aitkenhead *et al.* 1985: fig. 9).

Table 1 Numbers and distribution of productellid and plicatiferid species in the Craven Reef Belt.

SPECIES	No.	Pres.%	Facies	Locations
Argentiproductus margaritaceus	131	19·1	F/B, (Fr)	1, 2, 6, 7, 8, 9, 10, 11, 12.
Argentiproductus atripoides	33	2·5	Fr	10.
Productina cf. *pectinoides*	15	3·1	F/B	8, 9.
Plicatifera plicatilis	128	9·2	F/B, (Fr)	1, 2, 6, 10, 11.
Plicatifera pseudoplicatilis	173	15·4	F/B, (Fr)	1, 2, 5, 6, 7, 8, 9, 10.
Acanthoplecta mesoloba	311	34·2	F/B, (Fr)	1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12.
Admodorugosus cracoensis	18	2·2	F/B	8, 9, 10.
Geniculifera keyserlingiana	76	7·8	F/B, (Fr)	1, 2, 5, 6, 8, 9, 10, 11, 12.

Notes:

Number	Numbers of individuals recorded from initial collections of 20,941 brachiopods. As a result of preservational factors and some destructive analysis, not all the specimens have been retained in museum repositories.
Presence %	Percentage occurrence of the species in 357 localities sampled.
Facies	F/B = flank & bank; Fr = framework; (Fr) = very minor component.
Locations	1, High Hill; 2, Scaleber; 3, High South Bank; 4, Burns; 5, Cawden; 6, Wedber Brow; 7, Swinden; 8, Skelterton Hill; 9, Butter Haw Hill; 10, Stebden Hill, 11, Elbolton; 12, Thorpe Kail. See Brunton & Mundy 1988*b*: fig. 1.

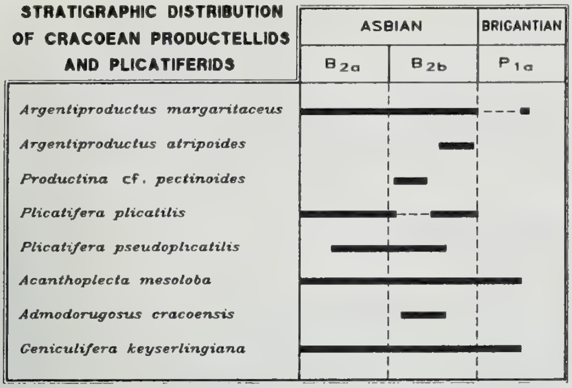


Fig. 72 The range of each species is based solely on their occurrence within the Craven Reef Belt and depends on goniatite calibration from the collections of DJCM (goniatite determinations by Dr W.H.C. Ramsbottom). Assemblage biozones of the *Beyrichoceras* Zone follow Riley (1990*a*).

The stratigraphical distributions of the productellid and plicatiferid species in the Craven Reef Belt, relative to the goniatite assemblage biozones, is shown in Fig. 72. *Argentiproductus margaritaceus, Acanthoplecta mesoloba* and *Geniculifera keyserlingiana* range throughout rocks of B_{2a} and B_{2b} Zone age and into P_{1a}. The latter two species are absent from strata of younger P_{1a} Zone age in which a low diversity, high abundance 'stressed' community (*Productus* community — Mundy, 1978, 1980) recolonized the buildups after a depositional hiatus, forming prolific shell beds on Stebden Hill and Elbolton. A single specimen of *Argentiproductus margaritaceus* has, however, been recovered from these beds.

Admodorugosus cracoensis typically occurs in strata of B_{2b} Zone age on Butter Haw and Skelterton Hill, as does *Productina* cf. *pectinoides*. The framework niche containing *Argentiproductus atripoides* on Stebden Hill is stratigraphically confined within strata interpreted as late B_{2b} Zone age.

Both *Plicatifera* species coexist in rocks of B_{2a} Zone age at Wedber Brow and High Hill, with *P. plicatilis* dominating, while in strata of early B_{2b} Zone age (well exposed on Butter Haw and Stebden Hill) *P. pseudoplicatilis* abounds with no record of *P. plicatilis*. In the overlying succession of late B_{2b} Zone age on Stebden Hill the latter species is again dominant, with insignificant numbers of coexisting *P. pseudoplicatilis;* in the Craven Reef Belt only *P. plicatilis* persists until the end of the B_{2b} Zone.

APPENDIX

The name '*Dorsirugatia*' was used, but not described, by Lazarev in 1990 (p. 80 & 145), where he placed it in the Productininae.

The full publication of *Dorsirugatia* Lazarev, 1992 took place while this paper was in preparation, and in a journal not easily obtained in Europe, so we add below the author's own description of the genus, type species and a brief discussion. This new Mongolian genus resembles *Productellina,* but until more of this British material becomes available the taxonomical relationships between the two must remain uncertain.

A NEW LATE DEVONIAN PRODUCTININID GENUS FROM MONGOLIA

Subfamily **PRODUCTININAE** Muir-Wood & Cooper, 1960
Genus ***DORSIRUGATIA*** Lazarev, 1992

1990 *Dorsirugatia* Lazarev: 80, 145.
1992 *Dorsirugatia* Lazarev, *in* Lazarev & Suursuren: 63.

Diagnosis. Small Productininae with wide ears, an inflated ventral valve and weak ribbing starting on both valves anterior of the umbones; spines are rare with indistinct rows of up to three at bases of the flanks.

Name. Latin, *dorsalis* = spinal or dorsal, *ruga* = wrinkle; referring to the ornamentation of the dorsal valve.

Type species. *D. tsagankhalgensis* Lazarev & Suursuren, 1992.

Discussion. *Dorsirugatia* differs from *Productellina* in its more strongly inflated ventral valve (B=0·6 as compared to 0·9; see below), larger ears, wide but weak costation, and possibly also in having a row of about three spines at the bases of the flanks. *Dorsirugatia* differs from *Productina* and *Argentiproductus* by its weakly developed costation, which is lacking on the umbonal regions. *Dorsirugatia* may be the earliest member of the subfamily which subsequently evolved into two lineages, recognized in younger rocks as *Productina* and *Argentiproductus.* It is difficult to determine the exact age of *D. tsagankhalgensis,* but judging by the stage of development of the costation this species is slightly older than *Productellina fremingtonensis* Reed and ?*Dorsirugatia rjausakensis* Nalivkin (p.101).

Dorsirugatia tsagankhalgensis Lazarev & Suursuren, 1992. Figs 73–77

1992 *Dorsirugatia tsagankhalgensis* Lazarev & Suursuren: 63; pl. 15, figs 10–12.

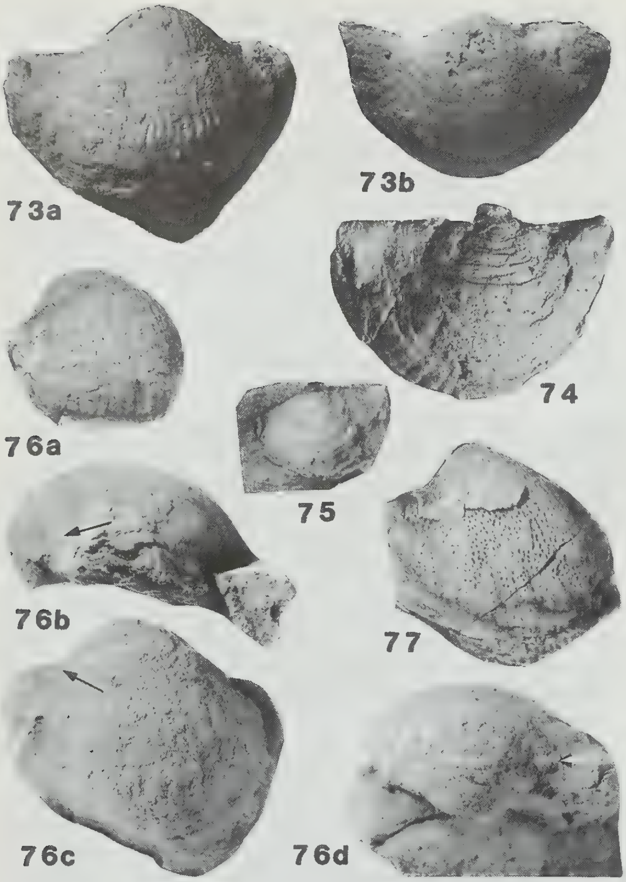
Name. The species is named after the mountain Tsagan-Khalgin-Ula.

Diagnosis. As for genus.

Type specimen. Palaeontological Institute, Moscow, N3385/1523, a ventral valve (Figs 73a, b) from 2 km east of altitude point 2202 m at the foot of Mount Tsagan-Khalgin-Ula, Gobi Altai, Mongolia. Uppermost Tsagankhalgin Formation (= late Wocklumaria Zone), near the top of the Famennian, Upper Devonian.

Material. About 50 other dorsal and ventral valves from the type locality.

Description. Shells are 8–11 mm long and 13–16 mm wide. They are subtriangular in outline, but with a protruding ventral umbo. Greatest width is at the hinge. Ventral umbones are quite strongly inflated (B=0·6, see below), with no sulcus; a rounded umbo extends about 1·7–2·0 mm beyond the hinge; flanks spread at about 45° from the hinge and the ears are large and almost flat. The short trail may be slightly carinate. Costae are lacking at the umbo and ill-defined on the rest of the valve; their width is 0·5–0·7 mm (rarely up to 0·9 mm anteriorly) and they are simple, without branching or



Figs 73–77 *Dorsirugatia tsagankhalgensis* Lazarev & Suursuren. All from the type locality in Gobi Altai, Mongolia (see p.117). Figs 73a, b, the holotype viewed anteroventrally and posteroventrally showing the weak ribbing, which is lacking from the umbo. Palaeontological Institute, Moscow, 3385/1523. ×3. Fig. 74, a dorsal valve exterior showing the late stage ribbing and lamellae. Palaeontological Institute, Moscow, 3385/1514. ×3. Fig. 75, the external mould of a dorsal valve showing the weak rugae and bases of lamellae. BD9423. ×2. Figs 76a–d, anterolateral oblique view of a ventral valve exterior (×2), and the same in lateral, ventral and posterior views (×3). Arrows indicate spine bases. BD9421. Fig. 77, an anterolateral oblique view of an incomplete ventral valve and part of its internal mould showing tuberculation. BD9422. ×2.

additions. Ribs are lacking on the ears. Spines are sparse and confined to the ventral valve; their bases measure 0·2–0·3 mm in width. There are no spines at the hinge, but there is an indistinct row of up to three spines at the base of each flank; the first spine is at 3 mm from the beak, the second at 4–5 mm and the third at 7–7·5 mm. Dorsal valves are deeply concave and non-geniculate. The dorsal ornamentation is rugose and lamellose, with lamellae 0·2–0·4 mm wide posteriorly and wider anteriorly; thin growth lines may be visible. Costae are ill-defined and positioned anteriorly.

Internally the ventral muscle markings are shallow and indistinct; teeth are absent and internal surfaces are tuberculate. Ear baffles are low and broad, continuing anteriorly as weak marginal ridges. In dorsal valves the cardinal process is V-shaped, with no alveolus. The cardinal ridge is wide and indistinct.

(The B factors above, in relation to valve inflation, represent a logarithmic growth spiral in which low numbers indicate tighter spirals, i.e. greater inflation umbonally so that the ventral lateral profile is more strongly convex.)

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The spores of *Leclercqia* and the dispersed spore morphon *Acinosporites lindlarensis* Riegel: a case of gradualistic evolution

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Synopsis. Variation in the spores of the lycopod *Leclercqia complexa* is described from the Middle Devonian of New York State, U.S.A. The spores are grouped into morphotypes forming a gradationary series representing two primary factors: ontogenetic maturity and natural variation. Comparisons are made with spores of *Leclercqia* sp. nov. from the upper Emsian of New Brunswick, Canada; with dispersed spores from various upper Emsian — lower Givetian localities; and with published records of *Acinosporites lindlarensis*. An inferred evolutionary lineage connects the two lycopod species, their spores, and dispersed spores of the *Acinosporites lindlarensis* morphon. These fossils show gradualistic evolution from the late Emsian to the early Givetian. *In situ* spores exhibit 'palingenesis': immature spores of *L. complexa* resemble the mature spores of *Leclercqia* sp. nov., thus connecting the two known plant/spore events in the *Leclercqia* lineage. Palynodemes have greater potential than miospore species alone for stratigraphical subdivision, because they represent temporally distinct records of individual plant species. The *Leclercqia* palynodemes exhibit two tendencies with time: a) curvatural spinae become larger, b) the proportion of spores with small distal sculpture decreases. The maturation sequence in *L. complexa* spores parallels the evolutionary history of morphotypes. Dispersed spores indicate that *Leclercqia* was widely distributed in late Emsian to Givetian times. *Acinosporites acanthomammillatus* and *A. macrospinosus* probably belong to related lycopods.

INTRODUCTION

Records of Devonian plants with in situ spores of complex structure and sculpture are becoming increasingly common. Spores of a monopseudosaccate spore genus, *Rhabdosporites* [*R. langii* (Eisenack) Richardson 1960], were first discovered in *Tetraxylopteris* (Bonamo & Banks 1967) and later, identical spores were found in another progymnosperm, *Rellimia* (Leclercq & Bonamo 1971, 1973). In contrast, the rhyniophytoid *Cooksonia pertonii* Lang 1937 (Fanning *et al.* 1988, 1992) has yielded crassitate spores belonging to four dispersed genera with different sculpture from two stratigraphical levels, the Upper Silurian (Downton Group +/- = Pridoli) and the Lower Devonian (Lower Ditton Group, lower but not lowest Gedinnian) of the Welsh Borderland. In the Downton Group, laevigate and verrucate spores, both with an equatorial crassitude, and belonging to the dispersed spore genera *Ambitisporites* and *Synorisporites* (*S. verrucatus* Richardson & Lister 1969) were found in the sporangia of *C. pertonii.* Associated spore masses (possibly of *C. pertonii*) contained structurally identical murornate spores with proximal papillae, *S. tripapillatus* Richardson & Lister 1969. The Lower Dittonian spores of *C. pertonii* have the same structure but are apiculate and belong to the miospore genera *Streelispora* and *Aneurospora*. The parent plants are apparently identical but their isospores, with similar structure, have dissimilar sculpture which changed through time from laevigate and verrucate-murornate to apiculate. A similar trend in sculpture is repeated in dispersed cryptospores and in miospores of several structural groups, from the Wenlock to the Gedinnian (Richardson & Burgess ms.). The earliest known trilete spores free from the tetrad appear in the Llandovery. They are laevigate with an equatorial crassitude (*Ambitisporites*) and are similar to some of the Downtonian spores of *C. pertonii*.

Leclercqia complexa Banks, Bonamo & Grierson 1972 and *Leclercqia* sp. nov. (Kasper unpublished) are more complex plants than *Cooksonia pertonii.* Some of the spores of *Leclercqia complexa* (lower Givetian) described below are closely similar to *in situ* spores in Kasper's material (upper Emsian) and can be placed in a single species of *sporae dispersae*, whereas in *C. pertonii* four different dispersed spore genera occur in apparently identical plants of two different ages.

The importance of this and similar studies of *in situ* spores cannot be over-emphasized. In the thirty years since Nau-

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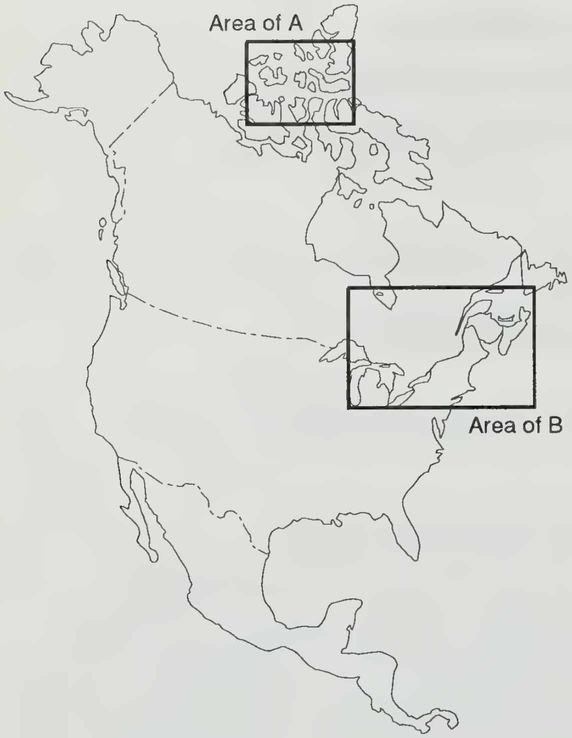


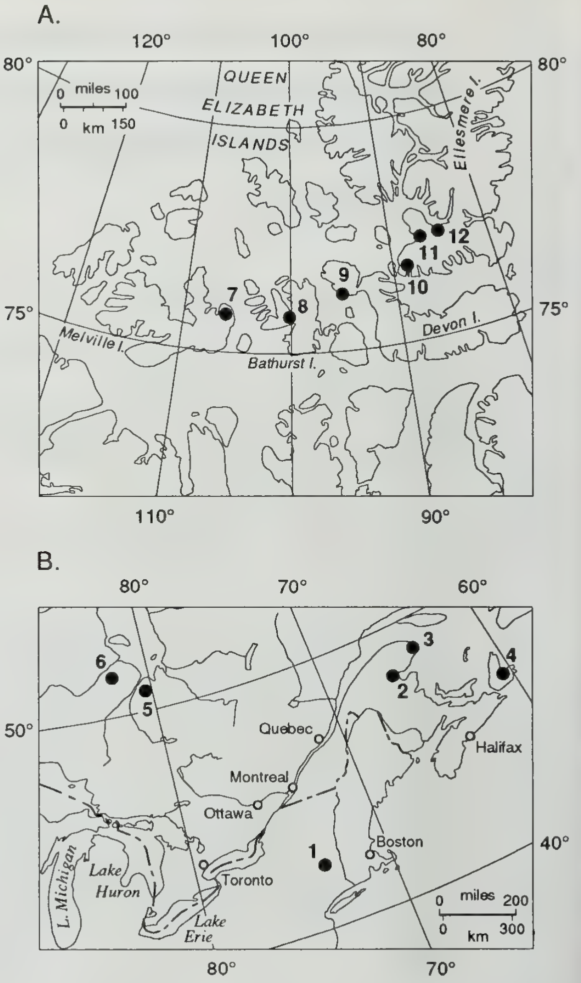
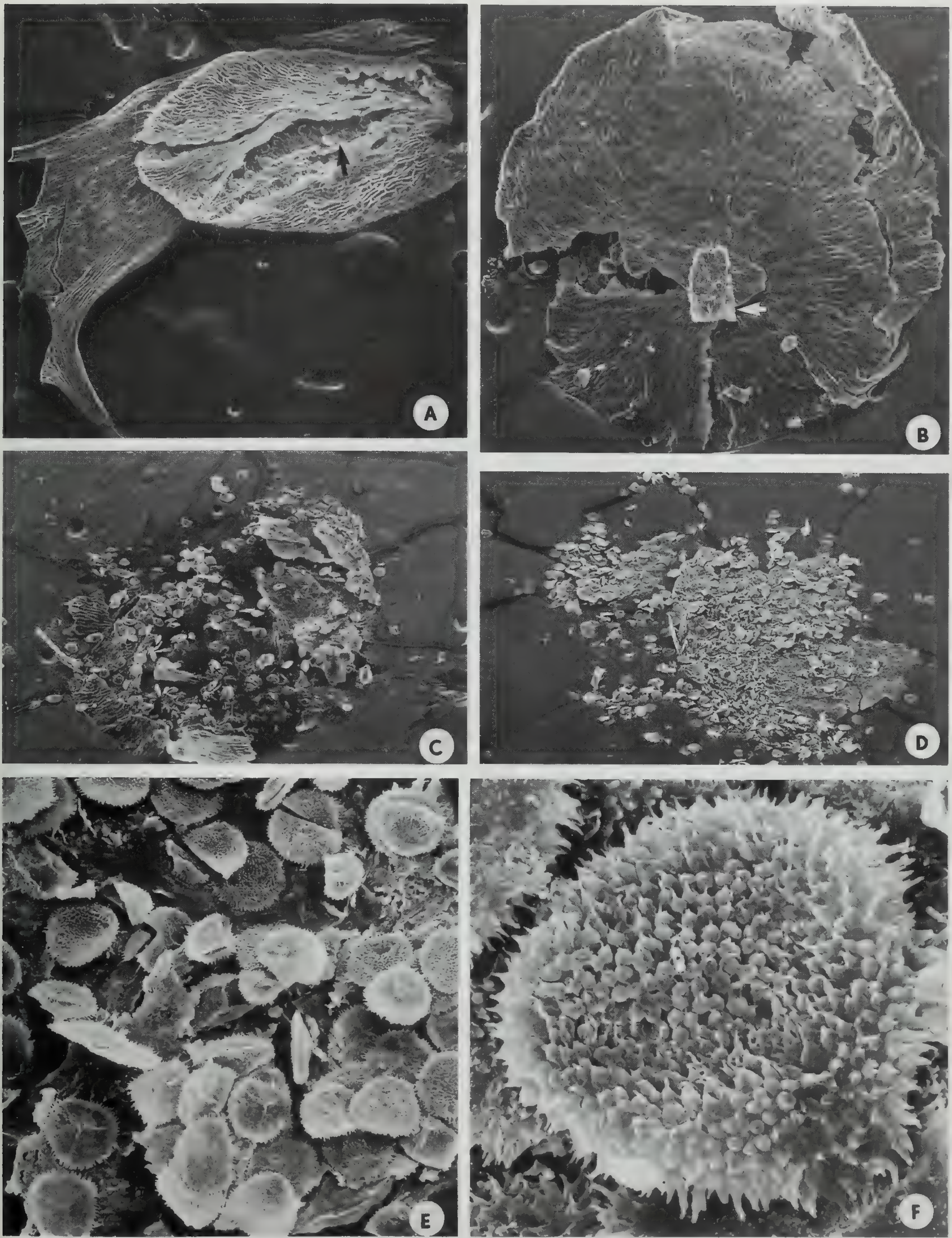


Fig. 1 Maps showing provenance of specimens. 1 — New York State (Blenheim-Gilboa); 2 — northern New Brunswick (Dalhousie Junction); 3 — Gaspé, Quebec; 4 — northern Nova Scotia; 5 and 6 — northern Ontario; 7 — Melville Island; 8 — Bathurst Island; 9 — Devon Island; 10–12 — Southern Ellesmere Island. For additional information, see Appendix I, Register of Localities.

mova (1953) published her classic work on the dispersed spores of the Russian Platform there has been a tremendous increase in the amount of data on Devonian *sporae dispersae* and their stratigraphical and geographical distribution. This information could, if better understood in an evolutionary context, vastly increase our knowledge of the evolution, distribution and habitats of Devonian land floras, all of which profoundly influenced the evolution of terrestrial animals (Shear *et al.* 1984). Dispersed spore records greatly exceed those of their parent plants, and the key to this treasure chest of data is the study of *in situ* spores: studies of the diversity of *in situ* spores and how they change in time may give clues to evolutionary pathways of dispersed spores and their parent plants which neither plants nor spores alone can give.

This paper describes the wide variety of spores present in numerous sporangia of two species of *Leclercqia*. The spores are easily identifiable in dispersed spore assemblages because of their distinctive, complex sculpture. Dispersed spores, many identical to those found *in situ*, were investigated from middle Emsian to lower Givetian strata of North America and are considered to belong to one morphospecies. Within this species we describe 15 informal variants referred to numbered types and subtypes. This sequence of assemblages of types we regard as a single species morphon. A morphon has been defined as 'a group of palynological species united by continuous variation of morphological characteristics' (van der Zwan 1979, p. 11; see also van der Zwan & Walton 1981). As form taxa and taxonomic levels are subjective, we are extending the morphon concept to include groups of informal units at any taxonomic level that are interconnected by continuous variation. By our definition some morphons may be intraspecific. Within the intraspecific morphon of *Leclercqia* spores, and spores inferred to belong to this plant genus, the morphographic ranges and proportions of types vary through geological time. At a particular geological horizon, the pattern of types and subtypes constitutes a palynodeme (Visscher 1971) which may be unique in its range of variation. For example, the lower Givetian palynodemes represented by spores of *L. complexa* are composed mainly of various subtypes within Type I, whereas in the dispersed spore

Fig. 2 *Leclercqia complexa*, scanning electron photomicrographs of sporangia and spores from Blenheim-Gilboa. (a) Sporangium attached to sporophyll showing *in situ* spores (arrow), 101A, tilt 70°, × 40. (b–f) One sporangium and its spores: (b) intact sporangium with portion of sporophyll attached eccentrically (arrow), 42A, tilt 60°, × 50; (c) upper half of sporangium with spores of Subtype IC, 42A, tilt 90°, × 40; (d) bottom half of same sporangium, 214, tilt 90°, × 40; (e) detail of spore mass in (d) of Subtype IC spores, 214, tilt 45°, × 200; (f) distal view of a single spore from (d) showing acanthomammillate distal sculpture, 214, tilt 22°, × 1,000.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assemblages from the upper Emsian and Emsian/Eifelian the spores of the palynodemes belong to subtypes of V and VI (Table 1 and Fig. 18).

Our use of the term palynodeme requires some explanation. We have three types of spore data. The first two (*in situ* spores, and spores from a single horizon and geographical location, i.e. +/- contemporaneously dispersed spores) are regarded as true palynodemes sensu Visscher (1971). The third set of data is heterogeneous and derived from multiple samples collected at several locations and/or horizons, but within a limited stratigraphical range. In order to distinguish these types of data in the text, assemblages from multiple localities/horizons (Fig. 1 and Appendix I) are referred to as 'palynodemes', e.g. the middle Emsian 'palynodeme' (Hudson Bay Lowlands). In the Eifelian — lower Givetian 'palynodeme' (Canadian Arctic), material is sparse, was collected from several localities and belongs to two adjacent spore zones (see Table 1). Nevertheless, such dispersed spore assemblage data are remarkably consistent (see Table 1) and therefore are included in our lineage along with true palynodemes. Though this situation is far from ideal, the data presented, consisting of two lycopod species, their *in situ* spores, and dispersed spores of the *lindlarensis* morphon, represent one of the most complete plant/spore lineages in the pre-Quaternary record.

Photomicrographs were taken with a Leitz Ortholux microscope and Orthomat and an ETEC Autoscan B-1 SEM with polaroid PN-55 film at the University Center at Binghamton, State University of New York (SUNY-B); Zeiss Photomicroscopes II & III and a Hitachi 8S800 Field Emission SEM using HP5 film at The Natural History Museum, London, previously the British Museum (Natural History) (BM[NH]). Spores were coated with carbon and gold palladium or with gold palladium alone (SUNY-B) or gold (BM[NH]).

In the descriptions and the figure captions, the letter following each SEM stub number (e.g. 92K) refers to a particular sporangium. SUNY microslides (e.g. 2002 M 14) bear collection numbers (2002) followed by M for maceration and then a sample number (14). BM numbers (e.g. BM 051956 [334.1a]) refer to negatives in the archives in The Natural History Museum, London, and the number following in brackets is the specimen number from the Paleobotanical Collection, State University of New York at Binghamton. These 'BM' combination numbers refer to spores obtained from the matrix surrounding *Leclercqia*. Samples 334.1a, 1b, 1c refer to separate samples from a single large block consisting of a thin layer with large axes of *Rellimia* (1c) intercalated between two thick layers with abundant *Leclercqia* (1a, b). Dispersed spores from the Blenheim-Gilboa outcrop and borehole (B1, B2, & B3) sequences have a sample number added (e.g. BM 050053 [B1/24]). B1/24 refers to sample 24 from borehole B1. Dispersed spores from Canadian localities (Appendix I) are keyed to Geological Survey of Canada locality and slide numbers, (e.g. locality A-008058/22) and those illustrated have been assigned GSC type specimen numbers (e.g. GSC 96756).

All these numbers and the microslide numbers for the dispersed and *in situ* spores are given in the figure captions or Appendix III. Locality information is provided in Appendix I. Figured specimens of SEM mounts from New York State are conserved in the type collections of the State University of New York at Binghamton. Dispersed spores from New York and Canadian localities are in the Canadian National Type Collection of Invertebrate and Plant Fossils at the Geological Survey of Canada, Ottawa.

BLENHEIM-GILBOA (NEW YORK) — *LECLERCQIA COMPLEXA*

Material

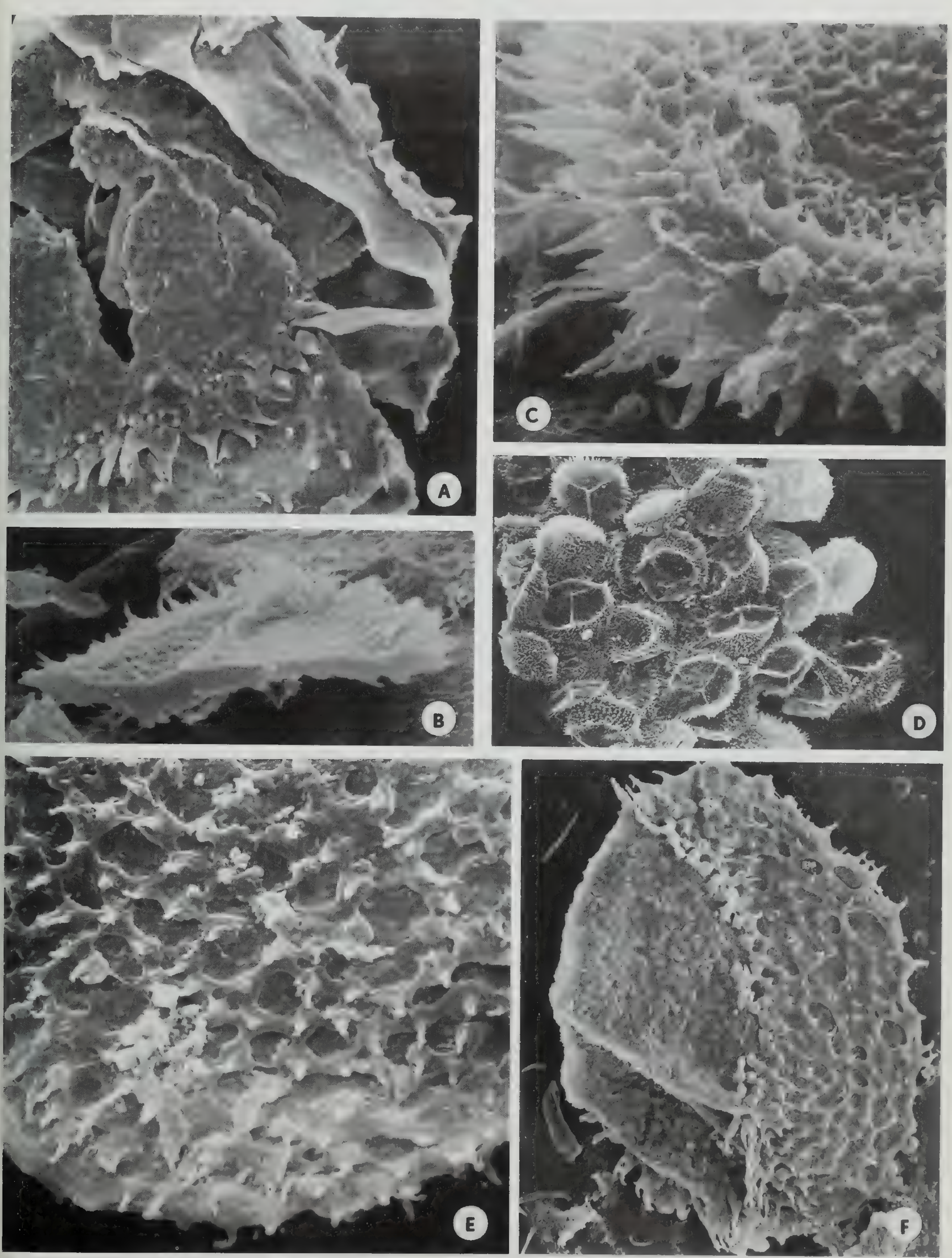
The present study of *in situ* spores is unique in that it is taking place in association with wide ranging studies on the geology, palaeontology, palaeobotany and palynology of marginal alluvial and marine sediments associated with the Catskill Alluvial Complex. Novel associations of arthropods and plant remains have already been revealed by this study (Shear *et al.* 1984, 1987, 1989a, b; Shear & Bonamo 1988; Norton *et al.* 1988; Kethley *et al.* 1989; Schawaller *et al.* 1991; Selden *et al.* 1991).

The locality data are given in Banks *et al.* (1972) for the original *Leclercqia complexa* locality at the Blenheim-Gilboa Pumped Storage Power Project. This site is now submerged by the lower reservoir. The additional localities sampled and discussed in this paper (see Appendix I) are: the cliff exposure behind the Power Plant and cores from borehole B1 drilled to a depth of 377.9 m and located 1143.8 m N60E of the reservoir near the Power Plant. The specimens are from the upper Panther Mountain Formation, Hamilton Group, Middle Devonian (Fisher *et al.* 1962, Rickard 1964, 1975). Our evidence for the age is discussed below.

Techniques for *in situ* spores

Small portions of sediment containing abundant *Leclercqia* axes were either transferred or macerated in hydrofluoric acid for three to four days, then given a hydrochloric bath for 24 to 48 hours. The material was neutralized by repeated washings with water containing a few drops of Kodak Photoflo. Photoflo, with a high pH, hastens neutralization and reduces the surface tension of the liquid, thus minimising the breakage of plant parts during manipulation. The resulting macerate was examined with a dissecting microscope. Even though the matrix appeared to contain only axes of *Leclercqia* with no intermixing of other genera, sporangia were chosen for further study only when their identity with *Leclercqia*

Fig. 3 *Acinosporites lindlarensis* and *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs; (a, f) dispersed spore; (b–e) *in situ* spores. (a) Equatorial view showing the two-layered structure of the exine, curvatural spinae and possibly vacuolate exoexine, BM 050056[B1/24], tilt 0°, × 1,700. (b) Equatorial view of broken spore showing 'homogenised' exine with distal and proximal exinal layers fused so that no lumen is visible, 214, tilt 45°, × 2,000. (c) Distal view showing typical evenly tapered curvatural spinae of Type I, 42A, tilt 90°, × 3,000. (d–e) Subtype IA spores derived from sporangium 91C: (d) part of a sporangial mass of spores of subtype IA showing curvatural spinae, trilete ridges and closely packed distal sculpture, tilt 45°, × 200; (e) detail of distal sculpture showing lacunae and biform elements on muri, tilt 45°, × 2,000. (f) Equatorial view of Subtype IA showing proximal, curvatural and distal sculpture, BM 051645 [334.1c], tilt 0°, × 1,200.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could be established either by their attachment to a sporophyll (Fig. 2a), or by their size and shape and the presence of an eccentric attachment pad (Fig. 2b; see also Bonamo *et al.* 1988).

Sporangia to be studied by light microscopy were first cleared one at a time in an embryological watch glass containing concentrated Schulze's solution (saturated solution at room temperature). Some sporangia were split in half or broken with needles to release the spore mass into solution. The clearing process was monitored under a dissecting microscope in a hood. Spores were removed with glass micropipettes, as they cleared, into a solution of Photoflo and water. After clearing (ca. 30 minutes) the spores and sporangial wall fragments were neutralised together in a watch glass by repeated washings with Photoflo and water, then mounted by micropipette on a coverslip in Clearcol. When the Clearcol hardened, the coverslip was affixed to a slide with Diaphane. Each slide contains hundreds of spores, all derived from a single sporangium.

Sporangia to be studied by scanning electron microscopy were also treated one at a time. They were removed from the neutralized macerate and placed on a stub with double sided Sellotape without clearing. Each sporangium was then teased apart with needles and the spores allowed to fall onto the tape. Thus sporangia and spores for SEM study underwent no acid or oxidative treatment other than that necessary to extract them from the rock matrix (HF/HCl). Several sporangia could be placed on one stub without intermixing the contents. The stub was numbered and each sporangium was given a letter designation (i.e. 92A designates stub 92, sporangium A). Some intact sporangia were first examined with the SEM (Fig. 2b) and then split in half. The portion originally fixed to the tape remained behind and was recoated (Fig. 2c); the other half was turned over and fixed to another stub (Fig. 2d–f). Thus stub 214 (Fig. 2d) supports the lower half and part of the spores of sporangium 42A (Fig. 2c). These methods permit comparisons of spores of the same and different sporangia.

Variation of *in situ* spores

Leclercqia complexa is apparently homosporous and has yielded spores similar to the dispersed spore species *Acinosporites lindlarensis* Riegel 1968. The three characteristic sculptural features of the spores are: i) a row of usually evenly tapered curvatural spinae (Fig. 3c) or biform tuberculae separating two types of sculpture differing mainly in size (Fig. 4a, 5a); ii) proximal sculpture of small interconnected elements that are sometimes biform (Fig. 3f, 6c, e, f); iii) variable distal sculpture with either 'beaded' muri or ridges (i.e. biform elements with slender mural interconnections) in a polygonal or irregular pattern (Fig. 4c, d), or sinuous and broad muri separated by rounded or irregular lacunae (Fig. 4a, b). The muri consist of basally interconnected biform elements. These sculptural elements have either expanded bases and slender apical coni or spinae, or narrower bases surmounted by parallel-sided or tapered coni. When such interconnected biform elements are crowded together the resulting sculpture is referred to as acanthomammillate (Fig. 2f, 9a–d). Trilete sutures are covered by variably elevated unpaired lips (tecta) sculptured by small coni (> 1μm; Fig. 5a, f). A distinct inner body (intexine) may be seen under the light microscope. One broken specimen, in fracture section under the SEM, reveals a thin intexine separated, at least in part, from the outer exoexine which appears vacuolate (Fig. 3a). The lacunose nature of the surface of some specimens in plan and the slender connections between the sculptural elements, seen best in profile, may be a result of the partial degradation of a vacuolate exine. An intexine is not always visible and its presence or absence may be diagenetically controlled (cf. Fig. 3a, b). A fracture section (Fig. 3b) shows a 'homogenised' spore wall with both the exinal layering and the spore lumen obliterated. In spite of the considerable variation found, most spores conform to the circumscription of the dispersed spore species *Acinosporites lindlarensis*. Although the end members of the variants are distinct they are joined by a plexus of intergrading intermediaries.

The morphographic variation discussed below is mainly between the spores of different sporangia. Spores from an individual sporangium, numbering well over 1,000, commonly belong to a single type or subtype. This study is based upon more than 200 sporangia.

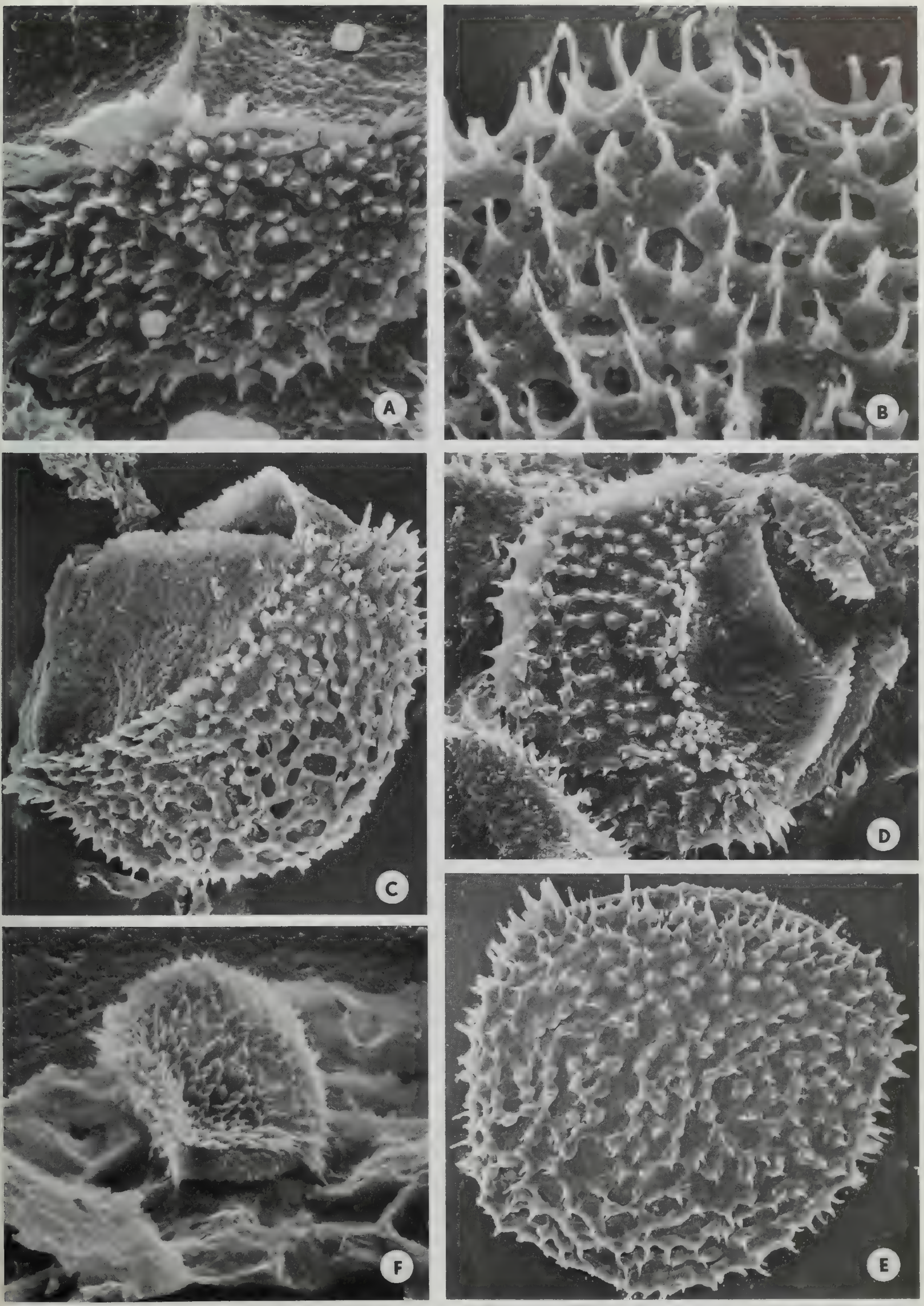
In assessing the range of variation, three factors have to be taken into account: 1) genetic variation; 2) ontogenetic variation (maturity); 3) preservational effects.

In situ spores described below show a number of basic features in common, but the variation is considerable and affects all three sculptural areas: proximal, curvatural and distal. The trilete mark is also variable and a central body is visible on some specimens. The spores have been arranged in six intergrading types and seven subtypes. The descriptions are based entirely on *in situ* spores, but when possible, dispersed spores from the rock matrix are included for comparison.

Type I. In most of the sporangia examined, Type I spores are dominant (Fig. 2c–f, 5e–f, 6a–f). The spores have relatively large (6–10 μm), uniformly tapered and pointed, curvatural spinae (Fig. 3c). The distal sculpture consists of biform elements (tuberculae surmounted by spinae) with coalescing bases (Fig. 4d) forming a variety of murornate patterns (Fig. 6b, 7b). The spinae over the distal surface of some dispersed Type I spores may include elements that have interconnected slender strands above the apparent spine bases (Fig. 5c, d). This feature may be preservational, related to degradation of a vacuolate outer exoexine. Proximal sculpture consists of small, crowded, biform elements. Type I is divided into three subtypes based primarily on their distal sculpture:

Subtype IA. The distal muri form irregular polygons

Fig. 4 *Leclercqia complexa* and *Acinosporites lindlarensis* from Blenheim-Gilboa, scanning electron photomicrographs; (a, d and f) *in situ* spores; (b, c, and e) dispersed spores. (a) Equatorial view of Subtype IA spore showing distal lacunae, 91C, tilt 45°, × 2,000. (b) Detail of part of the distal exine of a variant of Subtype IA showing elongate, biform spinae and lacunae, BM 0519578 [334.1a], tilt 0°, × 4,000. (c) Subtypes IA–B. Equatorial view, showing proximal trilete ridges, curvatural spinae and distal sculpture of muri surmounted by biform elements and surrounding lacunae. Distally the sculpture is like IA and subequatorially like IB, BM 051933 [334.1a], tilt 0°, × 1,300. (d) Subtype IB equatorial view showing 'beaded' distal muri surmounted by biform elements, 91C, tilt 45°, × 1,000. (e) Subtype IB distal view showing 'beaded' muri forming polygons surmounted by spinae and biform elements, BM 050076 [B1/24], tilt 0°, × 1,000. (f) Variant of Subtype IC in equatorial view showing elongate spinose terminations on the biform elements, 7, tilt 90°, × 1,000.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surrounding 'smooth' areas of the exine, or the muri are broad, not clearly differentiated, enclosing lacunae of variable size (Fig. 3e–f, 4a, 12a–c). Spinose terminations of the biform units may be elongate (Fig. 4b). This subtype intergrades with Subtype 1B, some spores showing ornament of both types (Fig. 4c). Proximally, the sculpture is reduced (Fig. 3f) and the trilete suture is covered by a low narrow ridge (tectum) sculptured by microconi (i.e. coni < 1 µm).

Subtype IB. The distal muri are 'beaded', i.e. the ridges are constricted between biform elements (Fig. 4d, 12d–f) and form irregular, sometimes incomplete, polygons (Fig. 4e). In sporangium 91C (Fig. 4d) the proximal sculpture is unclear, but some dispersed spores (Fig. 5a with SEM and slide 329/M/61 with light microscope) show well developed proximal sculpture and sculptured trilete ridges. Fig. 5a also illustrates evenly tapered curvatural spinae typical of Type I spores. Subtypes IA and IB can occur in the same sporangium, but IB is rare.

Subtype IC. The muri are sinuous but so crowded they obscure the lacunae and the murornate pattern (Fig. 5e, f, 6a, d). In sporangium 92B (Fig. 5e), only Subtype IC is present. Stubs 42A and 214 (Fig. 2c–f) are also from a single sporangium and consist solely of Subtype 1C. These spores, like IA and IB, have biform sculptural elements consisting of tuberculae surmounted by slightly tapered to more or less parallel-sided slender coni, spinae or bacula (Fig. 6a, b, d). Proximal sculpture is relatively large and biform, with minute bacula surmounting relatively large tuberculae that are interconnected at their bases (Fig. 6e, f). The unpaired lips (tecta) may form well-developed ridges sculptured by microconi (Fig. 5f). Subtype IC may occur in loose tetrads.

Each of these subtypes, IA, IB and IC, may include specimens having distal biform elements consisting of small tuberculae with elongate spinose terminations.

In one specimen, a variant of Subtype IC, the distal tuberculae and spinae are elongated (Fig. 4f). This form may intergrade with typical IC. Spores from sporangium 91D (Fig. 6b) show an acanthomammillate tendency in lateral compression, and in some specimens the spinose terminations are elongated but, in contrast to typical Subtype IC, the wall is partially lacunose (see also 6c).

Type II. Most curvatural spinae are delicate and baculate, evenly tapered, or biform, and the distal sculpture consists of ridges that are only slightly elevated.

Subtype IIA. The distal spinae are slender, baculate to slightly tapered, and supported by low ridges (Fig. 7a–c, f) with irregular lacunae (Fig. 7d). Some specimens are reticulate (Fig. 7b). Sporangium 101A contains some spores transitional between Types I and II. On typical Type II spores the curvatural elements consist of either tuberculae (Fig. 7c), some of which appear biform, or delicate slender spinae; other specimens in the same sporangium have prominent, evenly tapered, elongate curvatural spinae like Type IC (Fig. 7e). The proximal sculpture is apiculate to granulate, with elements similar to the other types, including Kasper's material described below. Some of the proximal elements are biform. Laesurae are covered by weakly developed ridges (tecta, Fig. 7a).

?Subtype IIB. Distal sculpture consists of stout biform elements on low ridges (Fig. 7g). Only one spore of this type was seen in this sporangium (92K) but a similar spore was seen in sporangium 92H.

Type III. The spores have slender curvatural spinae (Fig. 8a), and distal sculpture of grana (Fig. 8b), coni or pointed spinae on barely discernible ridges. The ridges form an irregular, reticulate pattern, or are separated by oval to irregular lacunae (Fig. 8a, c). Some spores have larger distal sculpture. Sporangium 169A contains some spores similar to Type II and one specimen in distal view (Fig. 8d) showing biform coni and ridges making polygons similar to Type 1.

Type IV. Specimens of Type IV have distal sculpture like that of Type III, but longer curvatural spinae (Fig. 8e; 5–7 µm compared with ca. 1.5µm on Type III). These specimens occur in the same sporangium as the Type III spores illustrated in Fig. 8a.

Type V. These spores have crowded, acanthomammillate distal sculpture and small, evenly tapered, or occasionally biform curvatural spinae. In the Blenheim-Gilboa sporangia, spores of this type are found only as tetrads, except for two specimens of Subtype VA separated from the sporangial mass.

Subtype VA (Fig. 8f, 9a). Curvatural spinae, seen on a few specimens only (Fig. 9b, arrow), are evenly tapered, tend to be small and may be biform. The proximal surface, rarely seen, bears reduced grana; no biform elements have been seen. Distal sculpture consists of crowded, smooth, sinuous ridges made up of biform elements of more or less equal diameter (Fig. 9c–d); ridges may be beaded but not crowded (Fig. 9d); biform elements consist of rounded bases (tuberculae) surmounted by slender coni or spinae. The trilete mark, simple sutures or low ridges, is rarely seen.

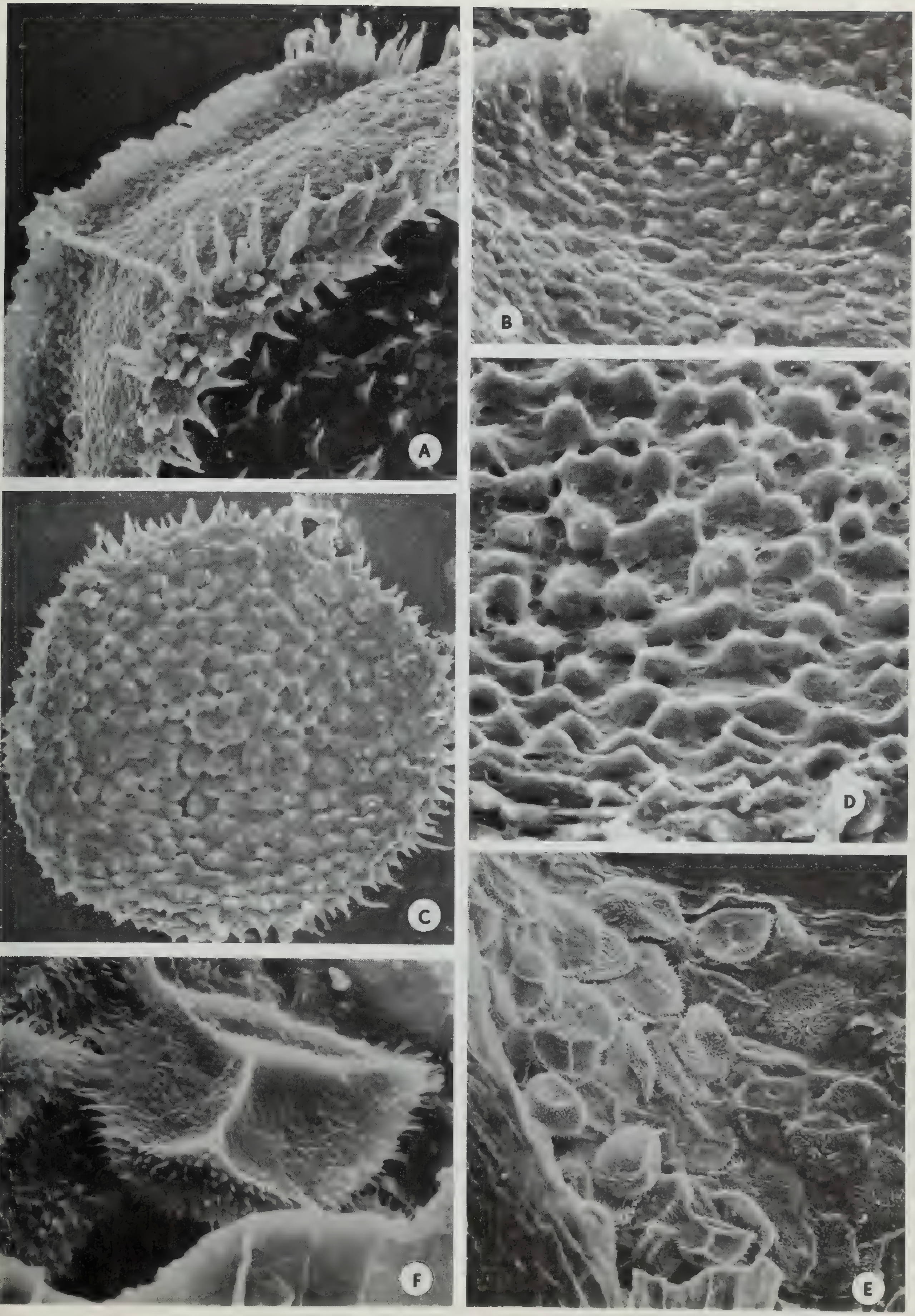
Subtype VB. The distal sculpture is smaller than in VA but is otherwise closely similar. The terminal coni of the biform elements are shorter over the distal pole than in the subequatorial region (Fig. 9e). In some tetrads the spinae are more elongate and are similar to Type VI (Fig. 9f). No trilete mark was seen.

Type VI. Spores occur only in tetrads (Fig. 13 a–c). Distal sculpture consists of small, crowded, biform elements, with slender, variable, elongate spinae but is otherwise similar to that of Subtype VB; muri faint or indiscernible. The sporangium is smaller than for other types. The trilete mark was not seen.

Variation of dispersed *Acinosporites lindlarensis*

Two kinds of material were examined: firstly, spores from bulk maceration of the matrix of *Leclercqia complexa* and from immediately adjacent sediments; secondly, spores dispersed in nearly 400 m of strata from the Blenheim-Gilboa Borehole (B1), penetrated to a depth of 377.9 m, and in outcrop sequences.

Fig. 5 *Acinosporites lindlarensis* and *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs; (a–d) dispersed spores; (e–f) *in situ* spores. (a–b) Subtype IB: (a) equatorial view, detail of proximal face showing sculptured, simple, trilete ridges, BM 051652 [334.1c], tilt 0°, × 2,200; (b) oblique view, detail of proximal polar apex showing simple trilete ridges and biform elements, BM 050053 [B1/24], tilt 45°, × 4,000. (c–d) Subtype IC, distal polar view: (c) showing close-packed interconnected ridges, BM 050041 [B1/24], tilt 0°, × 1,500; (d) detail of distal polar area of same specimen showing interconnected biform elements and microfoveolate nature of some of the interconnections, BM 050045 [B1/24], tilt 45°, × 3,500. (e–f) Spores from sporangium 92B: (e) part of a sporangial mass consisting entirely of Subtype IC spores, tilt 45°, × 300; (f) detail of a spore in oblique proximal polar view, tilt 45°, × 1,000.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An analysis of 133 spores picked out during bulk macerations of the rock matrix around *Leclercqia* from the Panther Mountain Formation gave the results illustrated in the first data set of Table 1.

The data in Table 1 may represent some selection by the observer (but see below) and may also be affected by the clearing techniques. Type I is dominant, Type V is absent and types II, III, IV and VI are rare, doubtfully present, or absent. Among the spores isolated from the sporangia, spores of Type I are dominant with Subtype IA most frequent among the subtypes.

Specimens of *A. lindlarensis* occur throughout the sequence of the Blenheim-Gilboa outcrop and borehole samples but are rare. They are abundant in the rock matrix surrounding specimens of *Leclercqia*. Subtypes IA and IB are numerically dominant among the spores found in both the matrix surrounding *Leclercqia* and in the borehole and outcrop samples. Subtype IA is dominant in all slides of specimens picked during bulk macerations of *Leclercqia*, except one in which over half the specimens belong to Subtype IB. Consequently, all the dispersed spore evidence is consistent with that from the *in situ* spores.

Morphotype inter-relationships

Suggested ontogenetic relationships between spore types are shown in Fig. 10. Types V and VI are found only in tetrads, and such spores are immature both in size and sculpture. The sculpture in Subtype VB and Type VI is smaller than in Subtype VA. Therefore, the spores VB and VI are assumed to be the most immature. In VA the distal sculpture consists of crowded, smoothly sinuous to beaded ridges, in part formed of biform elements (acanthomammillate) and sometimes interconnected by slender muri. This sculpture is closely similar to that of Subtype IC which sometimes occurs in loose tetrads.

Specimens of Type I are considered to include the most mature spores for three reasons. Firstly, they are the commonest spores found on bulk maceration of the *Leclercqia* matrix. Secondly, Subtype IA is also the most common subtype of the *in situ* spores. Thirdly, the spores of Type I include the largest specimens, and they are usually found in the largest sporangia which are partially dehisced.

Differences between Subtypes IA, IB, and IC may represent stages in maturation, natural variation, or preservational degradation. We consider that all three factors are involved, e.g. the differences between IA and IC may be due to a combination of maturity and degradation. In Subtype IC the distal sculptural elements are closely packed, whereas in Subtype IA the muri are separated and their elevation enhanced into the typical lacunose — reticulate pattern. At least two factors may be involved in this process: 1) swelling of the spore separating the bases of the muri and biform elements and 2) degradation of the intervening vacuolated outer layer of the exoexine. The exine pattern produced by the latter process indicates a structural control within the exine. The extension of these two tendencies plus the further expansion of the spore would result in the further separation of the ridges as seen in Subtype IB.

There is no evidence that Types II, III, IV and VI of *Leclercqia complexa* were ever dispersed. Types II, III and IV have poorly developed ridges and biform elements and may be immature forms. Spores of Type VI intergrade with VB and are regarded as the most immature spores in our normal maturation sequence (Fig. 10). As the sculpture in Types II, III and IV is less well developed than in Type V, and the spores have separated from tetrads, other factors may have controlled their development. Perhaps in such spores separation from a tetrad occurred before full development of the sculpture. There is some similarity between the distal regions of Types II and III and the distal polar exines of Types VC and VD from New Brunswick (p.134; Fig. 11a, b; Fig. 17a) in which the ridges are not developed and the spinae arise from a foveolate (i.e. not ridged) exine. Alternatively, some of these types may represent mature spores of natural small-sculptured variants. Type III has slender curvatural spinae, and in Type IV these spinae are stouter.

Are these spores (II, III, IV) normal but immature genetic variants, or do they represent the products of abnormal development within the sporangium? The fact that these specimens are rare in dispersed assemblages may indicate that such spores are not normally dispersed in upper Eifelian — lower Givetian assemblages. Subtypes of V and IC are either tetrads or are considered as developing spores held within an immature sporangium. The spores may not be dispersed until the sporangia are ripe and contain Type I (A–B) spores. The occurrence of other types in the *Leclercqia* samples may be due to the presence of sporangia that have been crushed to reveal immature spores.

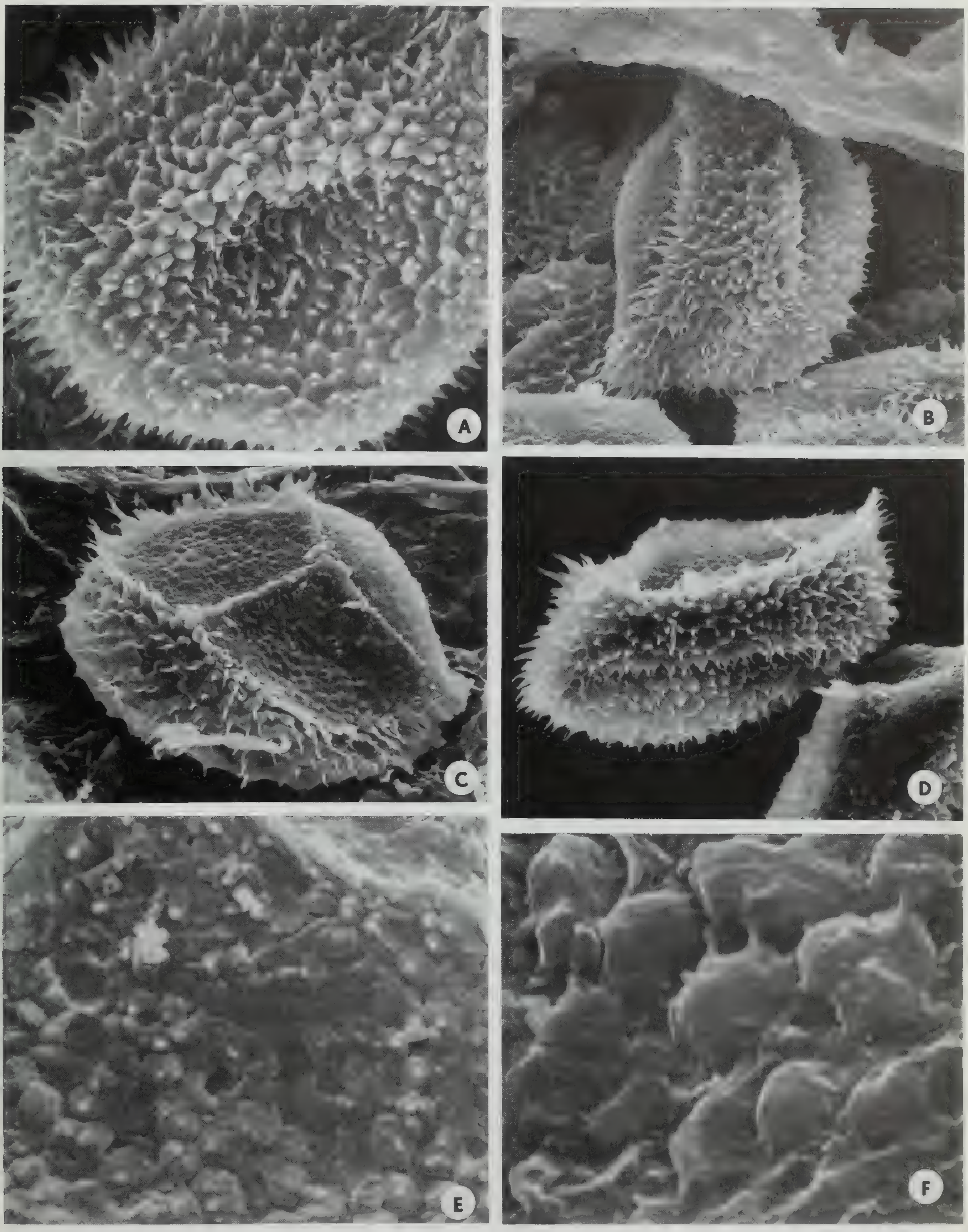
Forms with small sculpture may represent primary variants (Fig. 7a–d) [Type II, 101A]. These varieties are rare (see Table 1), but Type II is more common in older assemblages. The tendency to produce such spores is herein referred to as the 'parvulus' tendency.

One *in situ* specimen of Type I (Fig. 4f) was found with elongate tuberculae and spinae. It could be the result of natural variation, but similar spores have not been found in either the picked *Leclercqia* sample or the bulk macerated samples.

In situ and dispersed spores: structure, sculpture and nomenclature

STRUCTURE. All the *in situ* and dispersed spores appear to be azonate, but some show a variably separated intexine. Fracture sections give no indication of an equatorial or curvatural thickening. In some fracture sections (Fig. 3b), the proximal and distal parts of the exine are fused, and show no exinal stratification or lumen. In other broken specimens (Fig. 3a), a separated inner body (intexine) is present. Homogenisation owing to diagenesis may account for the apparent absence of an intexine in some of the New York specimens. Alternatively, these spores may be immature, and the presence of a

Fig. 6 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores, Subtype IC. (a) Distal view showing crowded biform elements, 92B, tilt 45°, × 2,000. (b) Equatorial view showing crowded distal biform elements with elongate terminal spinae, 91D, tilt 45°, × 1,000. (c) Tipped specimen showing trilete ridges, curvatural spinae and distal sculpture. Terminations of biform elements show little or no taper and are elongate, 45E, tilt 90°, × 1,000. (d) Equatorial view, showing crowded distal sculpture and long, evenly tapered curvatural spinae, 42A, tilt 0°, × 1,000. (e) Proximal apex showing trilete ridges and biform sculptural elements fused in groups, 214, tilt 45°, × 7,000. (f) Detail of proximal biform elements, 45E, tilt 90°, × 10,000.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body may characterize later stages of spore maturation.

In the dispersed and *in situ* spores prepared for light microscopy, oxidation may facilitate observation of the intexine. In order to evaluate these alternative interpretations, the dispersed spores of *Acinosporites lindlarensis* were compared with those *in situ*. In some of the preparations made for light microscopy, specimens showing a body were common. Preservation, maturation and oxidative treatment probably collectively determine whether or not the inner layer of the exine is observed. Some fractured specimens show a thin inner layer of the exine sometimes folded, and a thicker, structured outer layer that appears vacuolated under the SEM. These spores are regarded as azonate with an inner body (intexine) that is probably only attached proximally.

SCULPTURE. Equatorial and subequatorial spinae form a distinct, arcuate line joining the ends of the Y-rays, marking the edge of the contact areas and the position of the curvaturae perfectae. On most of the spore types these spinae are commonly evenly tapered, whereas most of the distal and subequatorial sculptural elements are biform. Specimens of Types IV and V, however, have shorter curvatural spinae, and some of these tend to be biform. A similar short-spined variant of *A. lindlarensis* var. *lindlarensis*, of early Givetian age, is figured by McGregor and Camfield (1976, pl. 5, figs 2, 3).

NOMENCLATURE. Streel (1972) placed spores from the rock matrix around *Leclercqia complexa*, and 'identical to the spore produced by this lycopod' (1972, p. 205), in the dispersed spore genus *Aneurospora*. However, we interpret these spores as azonate and believe they are best excluded from *Aneurospora*. Because some spinae 'bear a "cupule-like" thickening' at their apex, Streel (1972, p. 210) compared the spores with *Acanthotriletes heterodontus* Naumova 1953. Expansions of the spine tips have been found rarely in the present study. Except for the more common occurrence of the 'cupule-like' thickenings reported by Streel (1972), his spores are identical to *Acinosporites lindlarensis*.

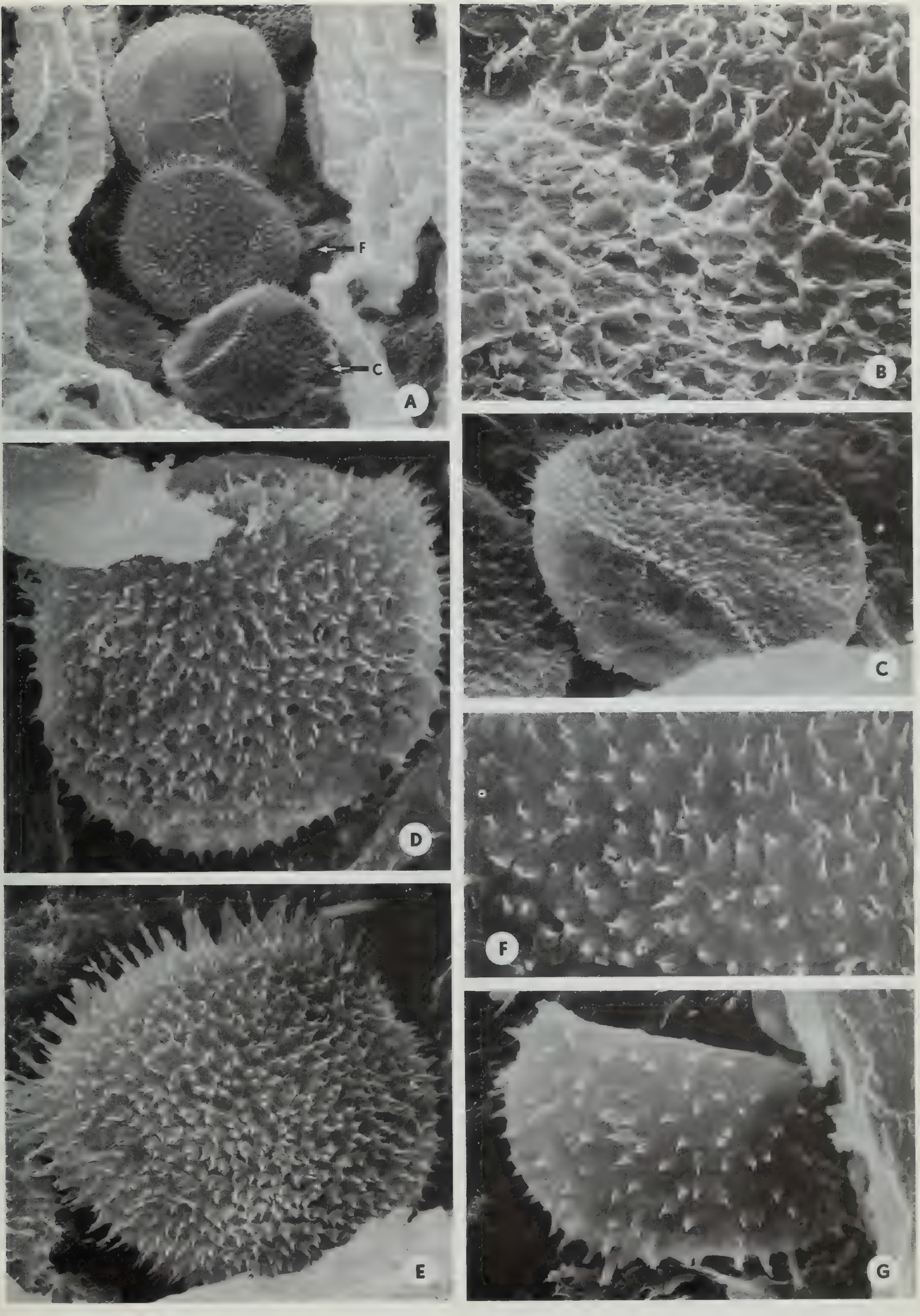
A distal sculpture of ridges with superimposed coni, spinae, or biform elements is the main feature of the genus *Acinosporites* and curvatural spinae are characteristic of *A. lindlarensis*. Riegel (1973) erected a second taxon, *Geminospora treverica*, for similar spores characterised by an intexine. McGregor and Camfield (1976) could find no difference between *A. lindlarensis* and *G. treverica*, and combined them. By establishing the variety *A. lindlarensis* var. *minor*, they also created the autonym *A. lindlarensis* var. *lindlarensis*. The type of the autonym is that of *A. lindlarensis* Riegel. *A. lindlarensis* var. *lindlarensis* has a known stratigraphical range from the middle Emsian to the middle Givetian.

Age of *Leclercqia* samples

Few long late Eifelian to early Givetian sections dated by other fossils and investigated palynologically, are available for comparison with the Blenheim-Gilboa sequence. Palynological dating of sequences of this age is further complicated by possible regional differences in spore assemblages. There are inconsistencies in the records of the first appearance of certain spore species between Arctic Canada and the Russian Platform on the one hand and between eastern North America and western Europe on the other (McGregor 1981, Richardson & McGregor 1986). Some of the differences involve key miospore events such as the incoming of *Samarisporites triangulatus* Allen 1965 and the 'flood' of *Geminospora* species (Richardson & McGregor 1986). At present the best conodont control of mid-Devonian spore sequences occurs in western Europe (Loboziak & Streel 1980; Loboziak *et al.* 1991), but in that region there are gaps in the spore succession, particularly in the Upper Eifelian. Sections from the Soviet Union (e.g. Arkhangel'skaya 1985b) and long sections in Arctic Canada (McGregor & Camfield 1982; McGregor in press) provide more nearly complete stratigraphical sequences but with less faunal control. The question is further complicated by the possibility of variations in the geographical occurrence of Geminospora caused by local, and possibly regional, environmental controls.

Loboziak and Streel (1980) have reported miospores from the Boulonnais, northern France. Their lowest assemblage, from the lowermost Blacourt Formation in Griset Quarry, contains poorly preserved specimens of several taxa in common with the upper part of the *devonicus–naumovae* Zone and the overlying *lemurata–magnificus* Zone. This lower Blacourt Assemblage is Givetian, according to associated conodonts. It is closely comparable to assemblages from the lower Blenheim sequence, which we believe are high in the *devonicus–naumovae* Zone. Spores from the middle and lower parts of this zone are not known in France. However, in several areas, Scotland (Richardson 1965 and unpublished), the Eifel (Riegel 1982) and Arctic Canada (McGregor and Camfield 1982; McGregor in press), more extensive sequences of the *devonicus–naumovae* Zone exist. In the Eifel region the uppermost Nohn to Freilingen formations correspond with the lower and middle *devonicus–naumovae* Zone (early to late Eifelian), whereas the overlying Ahbach Formation contains spores of the upper *devonicus–naumovae* Zone (Riegel 1982, fig. 1). *Geminospora lemurata* has now been found in two samples in the upper part of the Ahbach Formation, Müllert Member, just above the appearance of *Polygnathus ensensis ensensis* (Loboziak *et al.*, 1991). We therefore conclude that the Blenheim-Gilboa sequence is no older than late Eifelian (approximately middle *ensensis* conodont Zone of Ziegler 1979, fig. 6; *ensensis–obliquimarginatus* Zone of Loboziak *et al.* 1991, fig. 5).

Fig. 7 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores, (a–f) Subtype IIA, sporangium 101A; (g) Subtype IIB, sporangium 92K. (a) Enlargement of specimens at arrow in Fig. 2a. Spores within the sporangial wall, showing small, slender, curvatural spinae, weakly developed trilete ridges and small distal sculpture, tilt 90°, × 500. (b) Distal sculpture, showing weakly developed muri, surmounted by slender biform spinae and forming an irregular reticulate pattern, tilt 90°, × 2,000. (c) Enlargement of Fig. 7a, arrow c. Equatorial view showing weakly developed distal spinae and small distal sculpture, tilt 90°, × 1,000. (d) Distal view of spore showing lacunae, tilt 0°, × 1,100. (e) Transitional form similar to Subtype IC with well-developed curvatural spinae but smaller distal sculpture, tilt 45°, × 1,000. (f) Enlargement of specimen in Fig. 7a, arrow f. Detail of distal exine showing small lacunae and biform elements, tilt 0°, × 2,000. (g) Spore fragment showing low distal muri (ridges) and small, stout, biform elements and tuberculae, tilt 45°, × 1,000.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Brachiopod evidence from the Blenheim-Gilboa sequence indicates a late Givetian age (G. R. McGhee pers. comm.). Such a young age is not acceptable on palynological grounds.

A detailed account of the spore sequence at Blenheim-Gilboa will be published separately.

DALHOUSIE JUNCTION (NEW BRUNSWICK) — *Leclercqia* sp. nov.

Material

Plants belonging to a new species of *Leclercqia* with *in situ* spores have been discovered in the Campbellton Formation at GSC locality O–096376, 0.5 mile (0.8 km) west of Dalhousie Junction, New Brunswick (Kasper 1977). Comparisons between the New York and Dalhousie plants are limited because only a small amount of New Brunswick material is available. Plant material from this area was provided by Kasper who will publish details of his new species separately.

Variation of *in situ* spores

The following description is based upon the spores of only a few sporangia. The distal ornament of these spores closely resembles that of Type V from the Blenheim-Gilboa locality, but the curvatural sculpture is different.

Subtype VC (Figs. 11a–d, 17a, b). The spores bear typical acanthomammillate distal sculpture (cf. Blenheim-Gilboa Subtype IC and Subtype VA-B tetrads) of variably packed ridges, surmounted by small coni or biform coni and separated by lacunae (Figs. 11a, c, 17b). Alternatively, individual biform elements may be connected into irregular groups, consisting of a basal part with tapered sides, in profile, and surmounted by sharply tapered coni. In some specimens there are no ridges over the distal pole (Figs. 11a, e, 17a), but the exine is foveolate and supports slender coni or spinae; ridges occur towards the equator and appear beaded and markedly biform, but still crowded (Figs. 11b, d, 17a); distal subequatorial elements may be smaller and more crowded than those nearer to the distal pole. No evenly tapered curvatural spinae have been observed (compare with Fig. 9b of Blenheim-Gilboa) and the curvaturae are usually marked by a line of stout, rounded, weakly biform elements (Fig. 11b); sometimes these elements consist of a rounded, broad base bearing two coni or spinae. Proximal sculptural elements are smaller, crowded with polygonal bases and often distinctly biform (Fig. 11a). Tecta form low ridges sculptured by elements identical to those on the proximal face.

Subtype VD (Fig. 16a–d). Many specimens show a few biform curvatural elements with extended spinae that are larger than the distal biform elements (Fig. 11f, arrow, 16c) and are referred to as Subtype VD. The proximal sculpture is more prominent than that of Type V of the Blenheim-Gilboa material and consists of grana or tuberculae, many of which are biform. Proximal elements decrease in size towards the proximal pole. The trilete mark usually forms a low ridge on the exoexine (tectum) and lips or folds on the intexine (Fig. 11g) and in some specimens consists of simple sutures (Fig. 17c–d).

Variation of dispersed spores

The matrix surrounding *Leclercqia* sp. nov. and rock from other levels in the Campbellton Formation (see below), contains dispersed specimens of *Acinosporites lindlarensis*. Most of the spores show sculpture (Fig. 17d) closely similar to the acanthomammillate type seen in the *in situ* spores. In others, (Fig. 16f) the sculptural elements are more separated and approach those seen in Subtype IA. Small, elongate, biform curvatural spinae occur on some specimens from GSC locality O–096376. Proximal sculpture is well-developed and consists of scattered grana, sometimes interconnected into groups. The trilete mark consists of either simple sutures or trilete folds.

Age of *Leclercqia* sp. nov.

Dispersed miospores belonging to the lower *douglastownense–eurypterota* Assemblage Zone have been recovered from the beds containing *Leclercqia* sp. nov. (McGregor unpublished). The age of the plants is therefore late Emsian.

Comparison with the maturation sequence of *in situ* spores from Blenheim-Gilboa

Spores from near Dalhousie Junction resemble those of Type V from Blenheim-Gilboa. Among the dispersed spores are some with curvatural spinae that are mainly small and biform. The distal sculpture varies from that typical of Type V to a variety resembling Type IA, where the distal elements are arranged in small polygons. A further variant (Fig. 16f) was found with small distal sculpture of sinuous muri and biform elements ('parvulus' tendency). If our maturation sequence is correct (Fig. 10, p.138), *in situ* spores of *Leclercqia* sp. nov. most closely resemble, at least distally and equatorially, immature *L. complexa* spores that occur in tetrads. The dispersed spores from Dalhousie Junction show greater signs of development in terms of the proposed maturation series from Type VI, through V, to Subtype IA, but curvatural spinae are small and biform and not as well-developed as in IA.

DISPERSED SPORES OF THE *ACINOSPORITES LINDLARENSIS* morphon

In our palynological preparations

Dispersed specimens of *Acinosporites lindlarensis* have been examined from the following strata (see Fig. 1 and Appendix I): (a) Panther Mountain Formation, New York (see p.130 above); (b) Campbellton Formation, northern New Brunswick (samples collected by DCM and samples supplied to DCM by P.G. Gensel, J.D. Grierson and A.E. Kasper); GSC locality O–095530, *annulatus–sextantii* Assemblage Zone, middle Emsian; GSC locality O–098401, upper *annulatus–sextantii* Assemblage Zone, late Emsian; GSC localities O–096376, O–096385, O–098402, O–098403, and O–098404, lower *douglastownense–eurypterota* Assemblage Zone, late Emsian; (c) Battery Point Formation, Gaspé, Quebec (McGregor 1977); GSC locality A–007102, upper *annulatus–sextantii* Assemblage Zone, late Emsian; GSC localities A–005368 and A–007115, lower *douglastownense–eurypterota* Assemblage Zone, late Emsian; (d) Stooping River Formation, northern Ontario (McGregor & Camfield 1976); GSC

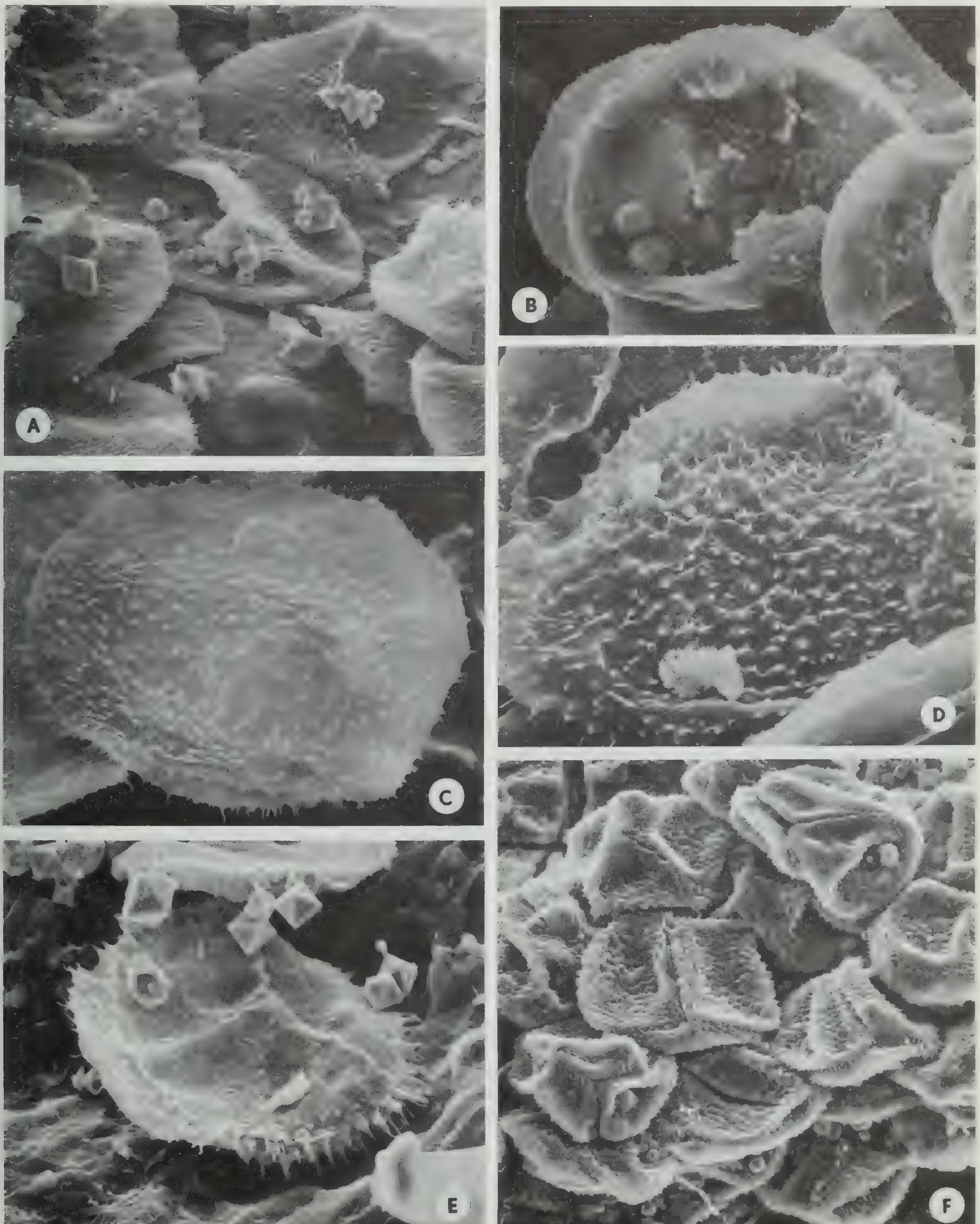


Fig. 8 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores; (a–d) Type III; (e) Type IV; (f) Type V; all figures × 1,000, except (f) , × 500. (a) Part of a sporangial mass showing spores with small curvatural spinae and distal coni, 45A, tilt 90°. (b) Detail of spores from another sporangium showing sculpture of grana and coni, 181A, tilt 0°. (c–d) Specimens showing larger distal sculpture borne by mural ridges or separated by lacunae, 169A, (c), (d) tilt 45°. (e) Specimen similar to Type III but with pronounced curvatural spinae, 45A, tilt 90°. (f) Sporangial mass of Type VA tetrads, 91A, tilt 90°, × 500.

localities A–008100 and A–008104, upper *annulatus–sextantii* Assemblage Zone, late Emsian; (e) Sextant Formation, northern Ontario (McGregor & Camfield 1976); GSC localities A–007850 and A–008785, lower *douglastownense–eurypterota* Assemblage Zone, late Emsian; (f) Malbaie Formation, Gaspé, Quebec (McGregor 1977); GSC localities A–007132 and A–007138, *velatus–langii* Assemblage Zone, early Eifelian; (g) McAdam Lake Formation, northern Nova Scotia (McGregor unpublished); GSC locality O–094437, lower *velatus–langii* Assemblage Zone, early Eifelian; (h) Williams Island Formation, northern Ontario (McGregor & Camfield 1976); GSC localities A–008057 and A–008058, *devonicus–naumovae* Assemblage Zone, early Givetian; (i) Cape De Bray Formation, Melville Island (McGregor, in press); GSC locality C–129628, *velatus–langii* Assemblage Zone, early Eifelian; (j) Bird Fjord Formation, Ellesmere Island (McGregor unpublished); GSC locality O–100909, *velatus–langii* Assemblage Zone, early Eifelian; (k) Bird Fjord Formation, Bathurst Island (McGregor unpublished); GSC locality O–100837, *velatus–langii* Assemblage Zone, early Eifelian; (l) Bird Fjord Formation, Devon Island (McGregor unpublished); GSC locality C–007678, lower *devonicus–naumovae* Assemblage Zone, mid-Eifelian; (m) Hecla Bay Formation, Ellesmere Island (McGregor unpublished); GSC locality C–091990, *velatus–langii* Assemblage Zone, early Eifelian; GSC locality C–091951, *devonicus–naumovae* Assemblage Zone, late Eifelian or early Givetian.

The ages assigned to these strata are based on their spore assemblages. For some of them, the age determinations have been supported by associated marine faunas, i.e. (d) conodonts (T. T. Uyeno, personal communication to DCM); (h) shelly faunas (Sanford & Norris 1975); and (j) conodonts (T. T. Uyeno, personal communication to DCM).

Specimens of *Acinosporites lindlarensis* from these localities were re-examined and classified into types and subtypes using the Blenheim-Gilboa spores for comparison. Table 1 shows the range of morphological variation of spores at each stratigraphic level (except levels with only rare specimens of uncertain assignment).

The following spore types and subtypes were either not seen or were rare at Blenheim-Gilboa:

Type I, Subtype ID (Fig. 14). The curvatural spinae are irregular, occasionally biform with bulbous bases (Fig. 14j). The spine bases are coarser than all other Type I spores, but in specimens ‘cf. ID’, some of the spinae are uniformly tapered. Distal sculpture consists of close-packed biform elements fused into groups (Fig. 14d). In some specimens the distal tuberculae are large and biform, in others the distal sculpture consists of ‘beaded’ ridges and irregular polygons similar to those of Subtypes IA and IB.

Type II (Fig. 15a, b, f). Curvatural spinae are small; biform elements are reduced and have faint interconnections. Type II from Blenheim-Gilboa exhibits a wide range of variation based on few specimens.

Subtype IIA (Fig. 15f). Curvatural spinae are evenly tapered, as Type I, and extended biform. The small distal biform sculptural elements are spaced with indistinct interconnections.

Subtype IIB. Stout biform elements occur on low ridges. Their bases may be crowded together with polygonal outlines.

Among the spores found in dispersed spore residues, specimens similar to subtypes IIA and IIB (Fig. 15 a–b) were found only in lower Eifelian sediments from Gaspé. They are listed as Type II in Table 1.

Type cf. V (Fig. 16e). Like Type V, but the distal sculpture is more widely spaced than typical Type V and some specimens bear discontinuous groups of elements.

Subtype VC (Fig. 17a–b). Like Type V from Blenheim-Gilboa, with biform elements fused into crowded, broad, sinuous ridges (acanthomammillate) but lacking curvatural spinae. Proximal sculpture consists of prominent biform units, appearing under the light microscope as scattered large grana, surrounded by discrete finely granulate elements, or with interconnections between biform units (seen only under SEM).

Subtype VD (Fig. 16a–d). Like VC but a few curvatural biform units show extended spinae. In contrast, Type V (Blenheim-Gilboa) has evenly tapered curvatural spinae, but these are rarely seen because the spores are in tetrads. In some specimens with biform curvatural spinae, the distal sculpture consists of biform elements with low broad bases so crowded together they form a polygonal pattern.

Type VI (see page 130). Small sculptured varieties found dispersed as separate spores are also referred to Type VI, but the *in situ* spores at Blenheim-Gilboa occur only in tetrads and precise comparisons are, therefore, not possible. Some dispersed specimens having more or less parallel-sided elements, and others with more rounded biform elements are referred to as ?Type VI (compare Figs. 17e and 13c).

Subtype VIA. No good curvatural spinae; distal sculpture small, beaded to crowded micro- and biform elements.

Subtype VIB. The curvatural spinae are slender. Distal sculpture varies from crowded to spaced.

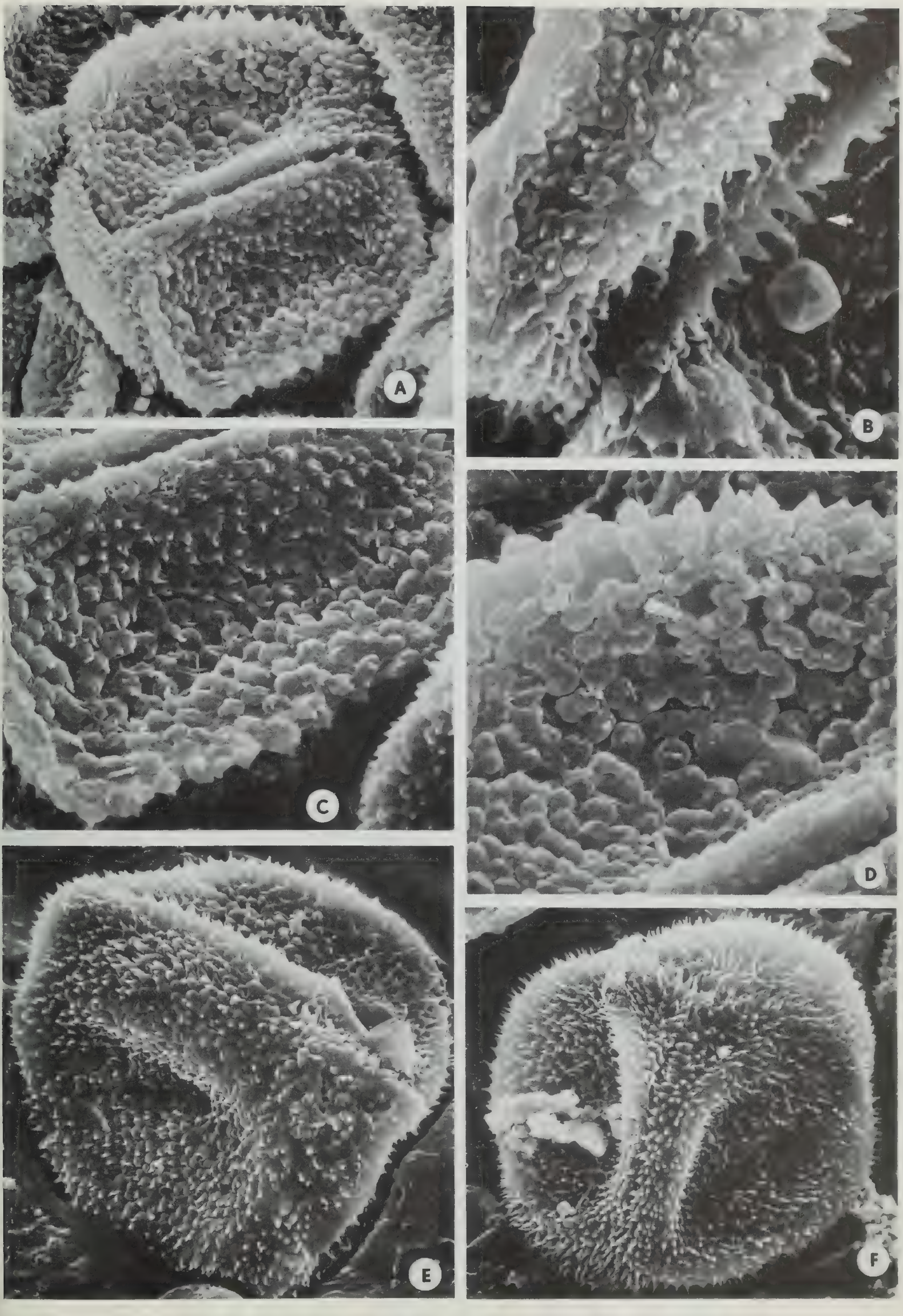
Subtype VIC. The curvatural spinae are a mixture of evenly tapered, biform and parallel-sided elements. Distal sculpture varies from crowded to spaced.

The spore data from the localities we have investigated have been plotted in stratigraphical sequence (Table 1). The table shows that for each successive palynodeme, the range of variation as expressed by the types and subtypes of *Acinosporites lindlarensis* is different. In the lower Givetian, Type I subtypes are dominant, whereas in the Emsian only subtypes of V and VI are present.

Examples in the literature

With few exceptions, the published records of *Acinosporites lindlarensis* are inadequately illustrated for detailed comparison and assignment to the informal types proposed herein. Nevertheless, the taxon is widely reported (see Appendix II) and specimens illustrated from the Emsian/Eifelian interval tend to have small, biform curvatural spinae (e.g. Riegel 1968, 1973) in contrast to the dominantly large spinae of the Givetian material.

Fig. 9 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores; (a–d) Subtype VA, sporangium 91A; (e) Subtype VB; (f) cf. Type VI, sporangium 91B. (a) Tetrad, tilt 45°, × 1,200. (b) Detail of spore in (a) showing small, evenly tapered curvatural spinae (arrow) and biform distal elements, tilt 45°, × 3,000. (c) Detail of distal sculpture in (a) showing crowded biform elements, tilt 70°, × 2,000. (d) Detail of (a) showing beaded ridges over distal polar area, tilt 45°, × 3,000. (e–f) Tetrads: (e) biform distal sculpture small and crowded, tilt 45°, × 1,000; (f) smaller specimen showing more elongate distal spinae, tilt 45°, × 1,200.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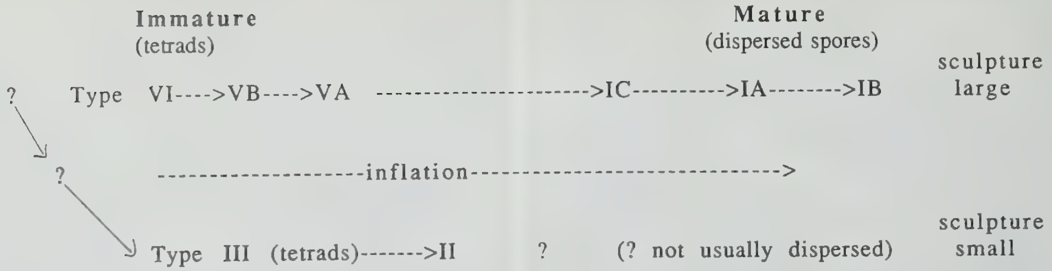

Immature
(tetrads)
Mature
(dispersed spores)
sculpture large
? Type VI---->VB---->VA ---------------------->IC---------->IA-------->IB
?
--------------------inflation----------------------------->
sculpture small
Type III (tetrads)------->II ? (? not usually dispersed)

Fig. 10. Maturation sequence of spores found in *Leclercqia complexa*. Inflation refers to increase in spore size as a partial cause of changes in sculptural pattern.

PATTERN OF EVOLUTION OF THE *LECLERCQIA* LINEAGE

The data in Table 1 and Fig. 18 show changes in the number and variety of types and subtypes from the *annulatus–sextantii* Assemblage Zone of middle Emsian age to the upper part of the *devonicus– naumovae* Assemblage Zone of late Eifelian age. Emsian assemblages have spores of basically two kinds, Types V and VI (Fig. 19a). Subtypes of Type V occur *in situ* in *Leclercqia* sp. nov. (Kasper) and are closely similar to immature spores of Type V from Blenheim-Gilboa. Spores of Type VI are regarded as the most immature in our Blenheim-Gilboa maturation sequence, but are not seen *in situ* in the Dalhousie material, possibly because of the smaller amount of material examined. However, subtypes of Type VI reflect a second tendency, the 'parvulus' tendency, seen in dispersed material in which some varieties have small sculpture. Spores showing the 'parvulus' tendency are rare, only 3 of 132 specimens among Blenheim-Gilboa dispersed spores (see Table 1, Fig. 19b), but are more common (see e.g. Fig. 17e, f) among Emsian dispersed spores (26 specimens) where they are almost numerically equal to spores of Type V (23 specimens).

In lower Eifelian assemblages from Gaspé (Malbaie Formation) and Nova Scotia (McAdam Lake Formation), spores of *Acinosporites lindlarensis* tend to have small curvatural spinae, and in both regions a few specimens have some evenly tapered and pointed spinae (cf. I, cf. IC, Fig. 15c–e, g, h). The occurrence of specimens comparable with Type I in the Eifelian marks the appearance of a character that dominates later (Givetian) assemblages. Other specimens from the above named formations have curvatural spinae of Type I and small sculpture on low ridges (? Subtype IIA). Spores with small distal sculpture and curvatural spinae are dominant (Type II, ?II) in both areas, but the McAdam Lake Formation contains two specimens belonging to VD with crowded distal sculpture and biform curvatural spinae.

Thirteen specimens were recovered from six early Eifelian to early Givetian localities in the Canadian Arctic (Cape De Bray, Bird Fjord and Hecla Bay formations). Spores from both the *velatus–langii* and *devonicus–naumovae* zones (Table 1) show two characteristic features: i) prominent curvatural spinae, some tending to be evenly tapered (cf. I, cf. IA) and others stout and biform (?ID, ID); and ii) small sculpture (Type VI).

Specimens from the early Givetian Williams Island Formation show morphographic variation like that of spores from Blenheim-Gilboa, with 46 out of 48 spores belonging to subtypes of Type I. The main differences from the New York specimens is that the majority of spores (41) are of Subtype ID, which possesses large biform curvatural spinae with bulbous bases. Some spores have crowded distal sculpture (IC, cf. IC) and others have evenly tapered spinae interspersed with biform ones. The two remaining spores belong to subtypes with small sculpture.

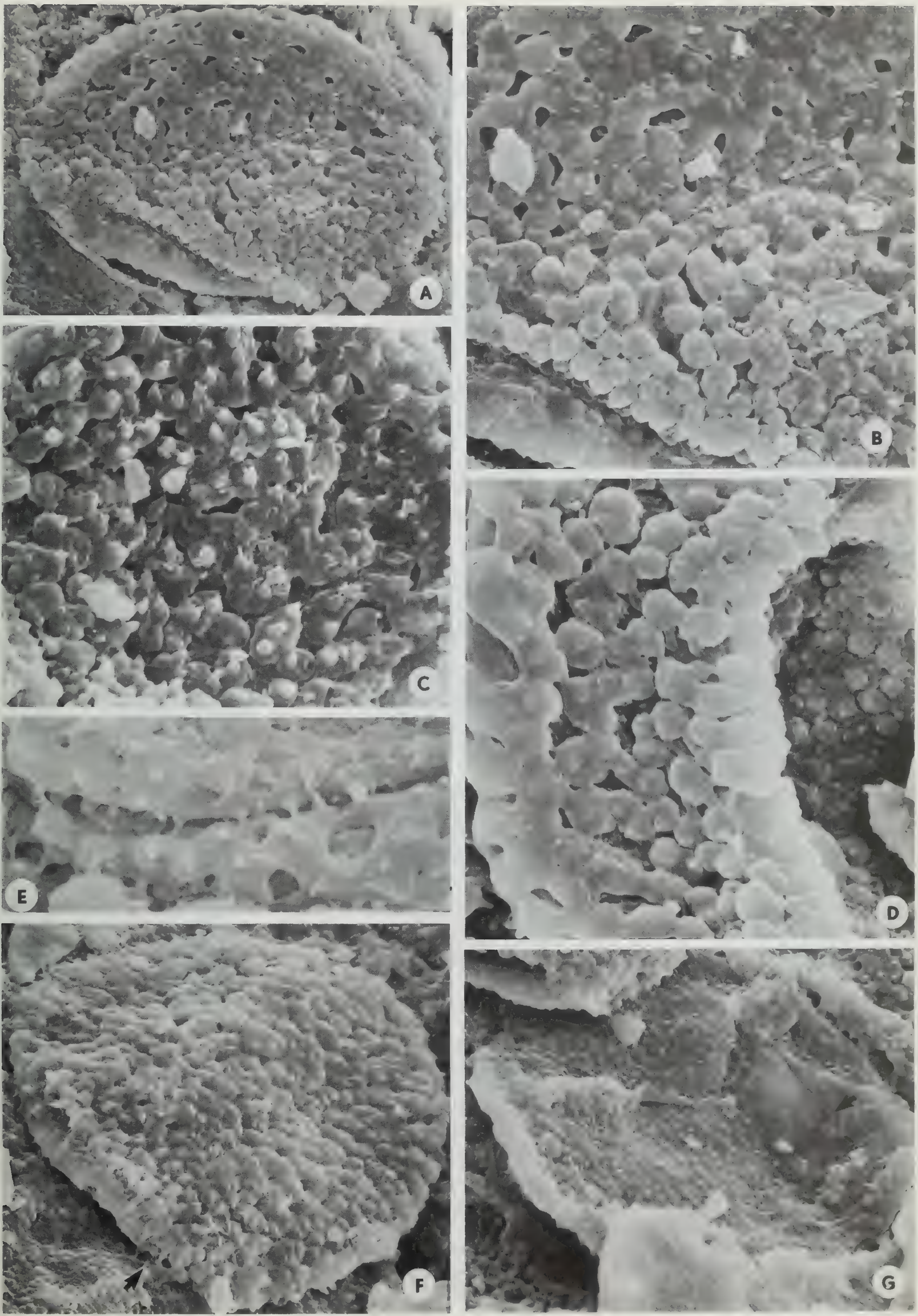
The succession of spore types shows an increasing tendency with time towards the development of large Type I (Fig. 18) curvatural spinae as seen in the material from Blenheim-Gilboa, with a secondary but persistent tendency to produce fewer dispersed spores with small sculpture.

COMPARISON WITH SPECIES OF DISPERSED SPORES OF SIMILAR SCULPTURE

In the Middle Devonian, a number of species first described from the Orcadian Basin of north-east Scotland (Richardson 1965), but subsequently reported from other regions, show some features in common with *Acinosporites lindlarensis*. These include spores with large sculptural elements, i.e. *A. acanthomammillatus* Richardson 1965, *A. macrospinosus* Richardson 1965, *Corystisporites multispinosus* Richardson 1965, and others with small sculpture, *A. parviornatus* Richardson 1965. *A. acanthomammillatus* shows a distal sculpture like that of Type V. In *A. macrospinosus* the spinose part of the biform unit is greatly extended forming large distal spinae superimposed on convolute ridges. The Scottish spores also have a larger size range than the spores in New York State.

Acinosporites is abundant in some strata in the lower part of the *devonicus–naumovae* Assemblage Zone. Here, in a

Fig. 11 *Leclercqia* sp. nov. from New Brunswick, Campbellton Formation, *douglastownense — eurypterota* Zone. Scanning electron photomicrographs of *in situ* spores of Type V; (a–e) Subtype VC; (f and g) Subtype VD. All figures tilt 45°, except Fig. e, tilt 90°. (a–b) Equatorial view showing foveolate distal polar area with coni and subequatorial area with murornate ridges, stub 257: (a) × 1,000; (b) detail of same spore, × 2,000. (c) Specimen showing biform elements superimposed on murornate ridges, stub 258, × 2,000. (d) Equatorial view showing curvatural elements with no spinose terminations, stub 267, × 3,000. (e) Detail of distal polar surface showing spinae and foveolate exine, stub 256, × 3,000. (f) Distal view showing small curvatural spinae (arrow), and crowded distal ridges, stub 257, × 1,000. (g) Proximal view showing relatively coarse sculpture over the contact areas and rupture of exoexine showing 'intexine' (arrow), stub 257, × 1,000.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part of the sequence dated as late Eifelian (based on spores), a third species of *Acinosporites*, *A. parviornatus*, is distinguished from the other two by its small, biform sculptural elements and ridges over the distal surface, an ornamentation similar to that in Type VI spores described herein. It lacks the curvatural spinae of some Type VI spores. *Corystisporites multispinosus* is also found in the Orcadian Basin. The distal ornament consists of biform spinae fused in groups. Such spores differ from *A. lindlarensis* in having lips elevated as an apical prominence, no visible wall separation and biform spinae all over the distal surface. The species is unlike any of the types and subtypes described, but reduction of the apical prominence and the distal biform spinae would produce a spore approaching Type I, with similarities to Subtypes IB and ID.

Thus, *Acinosporites* spp. in Scotland show morphographic features in common with certain types and subtypes of the *A. lindlarensis* morphon. Yet none of the species exactly match spores found *in situ*. Were such spores produced by other species of *Leclercqia*, or by plants of a related genus? The close similarity of some of the sculptural patterns, e.g. of *A. acanthomammillatus* and Type V suggests that their parent plants were related and perhaps diverged from a common ancestor in the Emsian. In this respect it is interesting to note that *Leclercqia* sp. nov. has spores that resemble in many ways *A. acanthomammillatus*, which first appears in the Lower Eifelian and perhaps represents the divergence of a separate *Leclercqia* species.

BIOLOGICAL IMPLICATIONS

The *in situ* spores from two species of *Leclercqia*, *L.* sp. nov. and *L. complexa*, show different ranges of sculptural variation. A comparison between the two complexes of *in situ* spores shows different combinations of types and subtypes (Fig. 19c, d). Additionally, dispersed spores contemporaneous with the *in situ* spores and from other beds of Emsian, Eifelian and Givetian age show a shifting pattern of types and subtypes (Fig. 18). Emsian strata contain types clustering around Kasper's *in situ* material, whereas Givetian spores show much more similarity to the *in situ* material from New York State. Thus both the macro- and microfossil evidence suggest evolutionary change from the Emsian to the Givetian. Further, the dispersed spore evidence from intervening stratigraphical levels (Eifelian to lower Givetian) shows that evolutionary change in the spores was gradual (Fig. 18, Table 1) and the pattern of types closely reflects the maturation sequence postulated for *L. complexa* (see Fig 10). The *in situ* spores of *Leclercqia* sp. nov. are closely similar to the tetrads (Type V) of *L. complexa* in the lower Givetian from New York State. Most of the dispersed spores associated with that plant are similar to Type V. Thus 'mature' spores from the Emsian most closely resemble 'immature' spores from the early Givetian (palingenesis), perhaps reinforcing the genetic relationship between *Leclercqia* sp. nov. and *L. complexa*. *L. complexa* has also been described from the Givetian of Germany and Australia and the lower Givetian of Belgium (Fairon-Demaret 1974, 1980, 1981). Similar forms (*L.* cf. *complexa*) have been described from older strata (lower Eifelian of Belgium, Fairon-Demaret 1981). A few dispersed spores from the matrix of the Belgian material are illustrated by Fairon-Demaret (1981, Pl. 1, figs 7–10) and appear to belong to Type I.

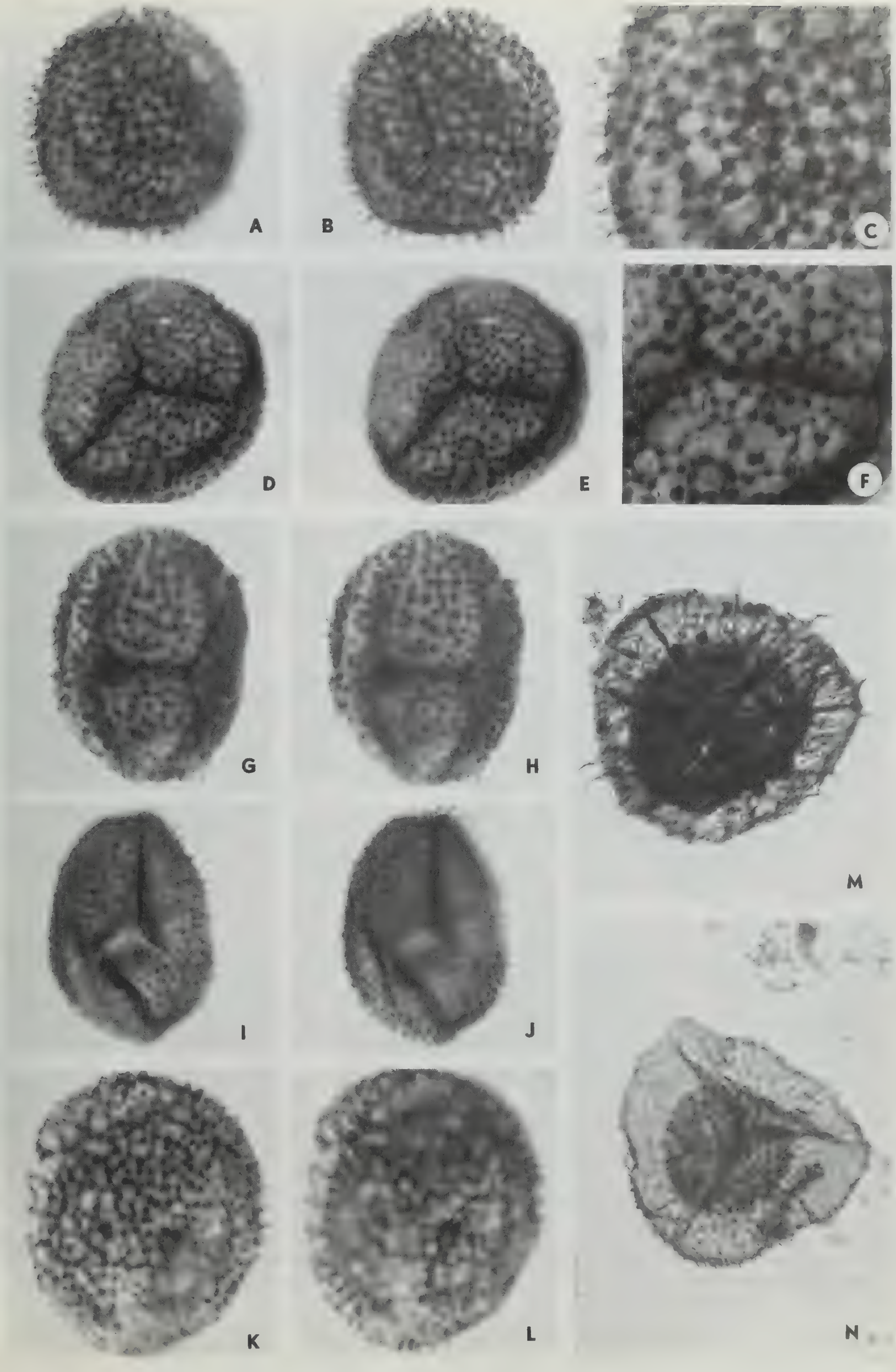
STRATIGRAPHICAL IMPLICATIONS

Within the morphon *Acinosporites lindlarensis* the component types and subtypes intergrade and within each stratigraphical interval the plexus of spores (palynodeme — 'palynodeme') is different. The stratigraphical range of *A. lindlarensis* (middle Emsian to lower Givetian) embraces nine palynodemes — 'palynodemes' (Table 1, excluding those of *Leclercqia complexa* and *L.* sp. nov. spores) and each is apparently unique, providing greater potential for stratigraphical refinement than the undivided taxon *A. lindlarensis*.

Evenly tapered curvatural spinae are rare and small in the Emsian and occur more abundantly in Eifelian rocks. Larger, typical Types IA, B, and C curvatural spinae are most common in Givetian strata. As the overall trend is towards increase in the prevalence of spores with such spinae, the Williams Island Formation with its predominance of specimens with biform curvatural spinae may be older than Blenheim-Gilboa sediments, where spores with large, evenly tapered curvatural spinae predominate. An alternative hypothesis is that this different variation in the two lower Givetian samples is due to geographical factors, but our data do not allow us to explore such a possibility further. Thus, the spores of the two *Leclercqia* species appear to have undergone palingenesis and gradualistic evolution between the late Emsian and early Givetian. The early stages of spore maturation in the Givetian sporangia repeat the morphology of mature spores in the upper Emsian. There is evidence for a lineage of spores from the Emsian to the Givetian. Emsian specimens have larger proximal sculpture, a partially foveolate distal exine, subequatorial closely packed ridges and small, sometimes biform curvatural spinae. In the mature spores of *L. complexa* from the Givetian, large, evenly tapered, curvatural spinae are dominant and biform spinae are rare. The distal ornament in dispersed spores throughout the Emsian-Givetian sequence is variable, showing a similar range of variation to that seen in the Blenheim-Gilboa material. For example, both beaded ridges and closely packed sculpture occur in earlier 'palynodemes'. Spores with barely discernible ridges connecting the biform elements occur throughout most of the sequence, and are most abundant in the Eifelian.

Type VI spores with small sculptural elements ('parvulus' tendency) are most abundant in the Emsian, where they may represent a natural variant. These spores are rare in dispersed

Fig. 12 Dispersed spores from Blenheim-Gilboa, specimens photographed using Nomarski differential interference contrast on a Zeiss Photomicroscope; (a–l) *Acinosporites lindlarensis*. All magnifications × 500 except (c) and (f) × 1,000, (m) and (n) × 250. (a–c) Subtype IA, distal view, lacunose: (a–b) general view; two different focal levels. (c) detail of distal sculpture in plan. (d–f) Subtype IB, distal view, beaded ridges: (d–e) general view, two different focal levels; (f) detail of distal beaded ridges in plan. (g–h) cf. Subtype IB, distal view at two focal levels to show sculpture. (i–j) Subtype I. (k–l) Subtype I, distal view at two focal levels. (m) *Spinozonotriletes* sp. cf. *S. naumovae* (Kedo) Richardson 1965. (n) *Calyptosporites* sp. cf. *Grandispora libyensis* Moreau-Benoit 1980.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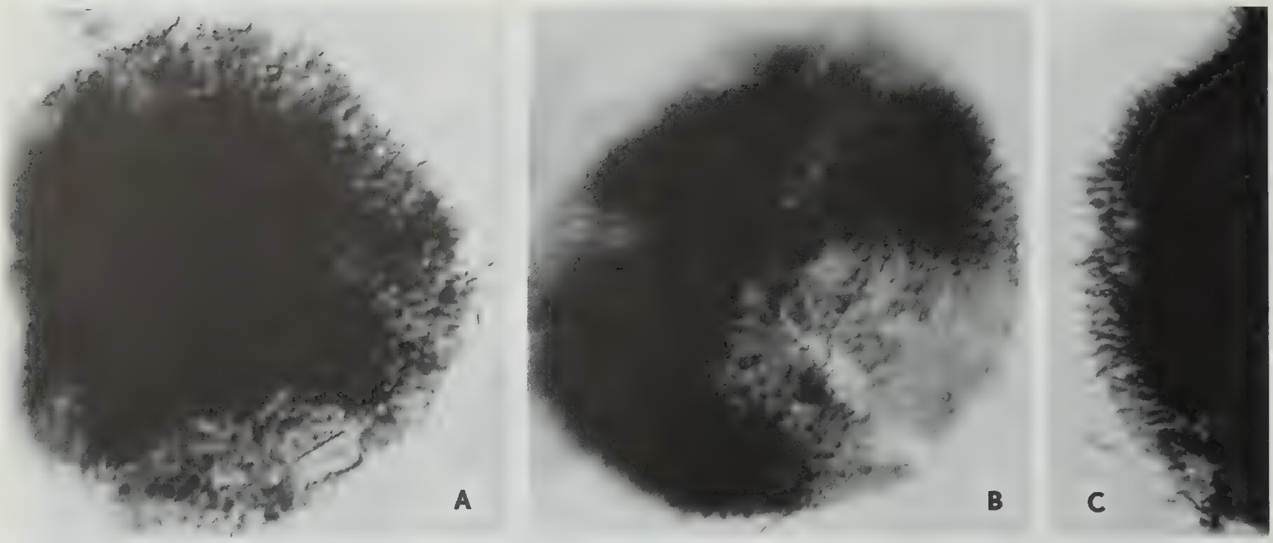

Fig. 13 *Leclercqia complexa* from Blenheim-Gilboa, light photomicrographs of *in situ* Subtype VI tetrads. (a) Tetrad showing sculpture of small biform elements. (b) Tetrad showing crowded bases of biform elements. (c) Detail of distal sculpture showing extended spinae on small biform elements.

assemblages at Blenheim-Gilboa, where they may represent an immature phase.

The dispersed spore record could now be checked for all of these features. Unfortunately, most publications showing this species contain photographs of only a few specimens so there is no indication of the range of variation at any particular horizon. Cramer (1969, pl. 2, fig. 27) illustrated a specimen that probably belongs to Subtype IA/IB, from the Eifelian to ?lower Givetian *Gosseletia* Sandstone Formation of north-west Spain. Riegel's (1973, pl. 19, figs. 11–16) spores from the Eifelian of Germany show more crowded distal biform elements, resembling Kasper's Emsian spores and Type V. Like Kasper's material, that from the Rhineland has prominent proximal sculpture. *Geminospora treverica* from the late Emsian and early Eifelian (Riegel 1968) has some resemblance to specimens that are rare in Blenheim-Gilboa. Some specimens of *Acinosporites lindlarensis* (McGregor & Camfield 1976, pl. 5, figs. 2–3) have small curvatural spinae and more discrete distal biform elements, or elements fused in small groups (ibid, fig. 5). Samples of Emsian and Eifelian age that contain abundant *A. lindlarensis* are needed so that the range of variation can be compared and the pattern of change in the lineage determined. Present indications are that taxonomic subdivisions of this lineage would be stratigraphically useful. Types V and VI could be used to subdivide the Emsian and Types I and II the Eifelian and lower Givetian. Knowledge of the range of variation seen in *Leclercqia* spores underlines the importance of describing the range of intraspecific variation in dispersed spore assemblages, from both the evolutionary and the stratigraphical points of view.

SUMMARY AND CONCLUSIONS

Dispersed spore assemblages from middle Emsian to lower Givetian strata include a succession of intraspecific 'palynodemes' of *Acinosporites lindlarensis*. Each 'palynodeme' illustrates a range of variation that is unique in the sequences examined, and there is a morphological 'continuum' with the *in situ* spores of two species of *Leclercqia* of different ages. Mature dispersed spores of *Leclercqia* sp. nov. (Emsian) have a striking resemblance to presumed immature spores (Type V) of *L. complexa* (Givetian). Immature spores of *Leclercqia* sp. nov. are distally foveolate and have a subequatorial sculpture similar to that of *A. acanthomammillatus*. The pronounced similarity between the sculpture of Type V and its subtypes, and *A. acanthomammillatus* may also indicate close genetic affinity between the parent plant of *A. acanthomammillatus* and *L.* sp. nov. We can speculate, firstly, that the ancestors of *Leclercqia* sp. nov. may have borne foveolate spores with small distal coni and secondly, that in Eifelian time a related lycopod with spores of the species *A. acanthomammillatus* also existed.

Data in Table 1 may indicate either gradualism or punctuated equilibria, but when these data are grouped as in Fig. 18 they appear to indicate gradualism. We prefer gradualism

Fig. 14 *Acinosporites lindlarensis*, light photomicrographs of dispersed spores. All from Williams Island Formation, *devonicus — naumovae* Zone, except (f) , Campbellton Formation, *annulatus — sextantii* Zone. All magnifications × 1,000. (a–b) Typical Subtype ID, polar compression: (a) proximal view showing biform and evenly tapered curvatural spinae, small Y-folds and proximal sculpture; (b) distal view showing crowded, coarse, biform elements. (c) Subtype ID, equatorial view, fragment of a broken spore showing irregular, biform, slender spinae. (d–e) Subtype ID, distal view: (d) plan view of crowded, broad-based elements in rows interconnected by slender muri; (e) biform elements in profile with broad basal rounded 'tuberculae' terminated by slender coni. (f) Atypical specimen in proximal polar view, showing large, broad, short, curvatural elements similar to VC and distal sculpture of crowded small elements similar to Type VI (parvulus tendency). (g–i) Subtype ID, distal polar view: specimen with small, crowded acanthomammillate distal sculpture at three focal levels showing: (g) small biform sculpture; (h) thin intexine; (i) biform curvatural spinae. (j) Subtype ID, proximal polar view, showing large typical biform, broad-based curvatural spinae.

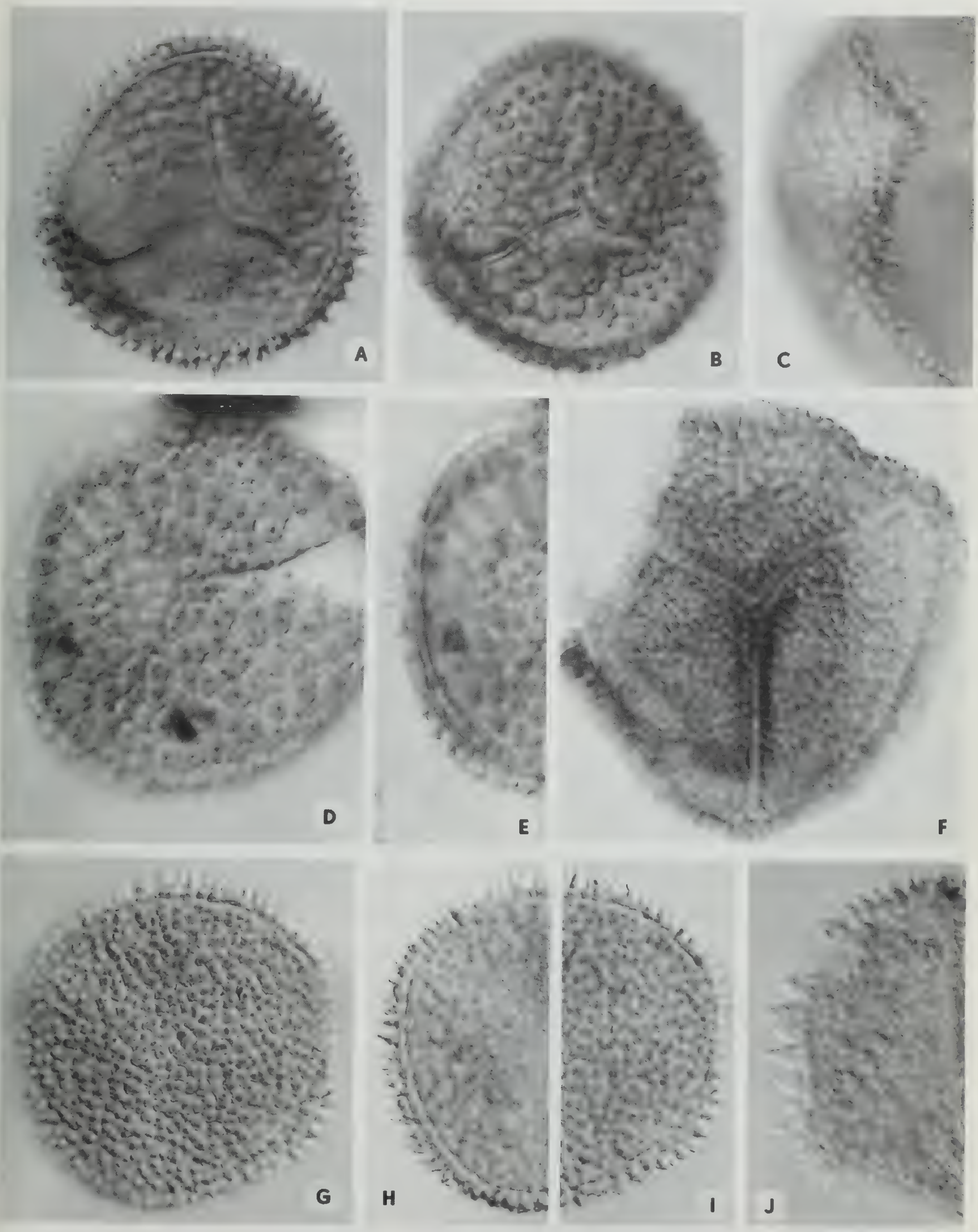
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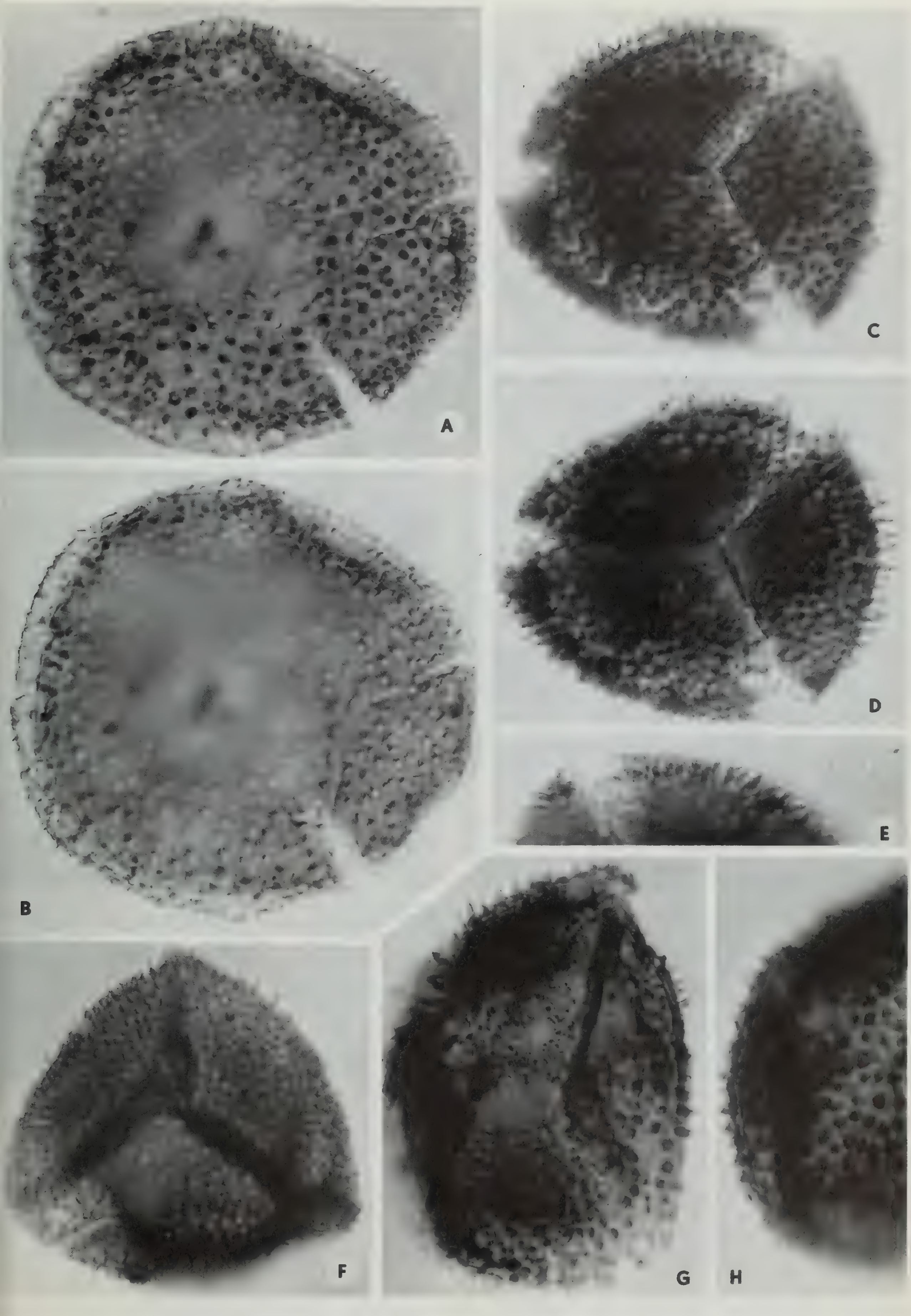
Table 1 *Acinosporites lindlarensis* types and subtypes: pattern of variation in 'Palynodemes' of different stratigraphical ages from Canada and New York State.

I	IA	IA/B	IB	IC	IA/C	ID	II	III	*V	*VC	VD	VI	VIA	VIB	VIC	TOTAL
Panther Mountain Fm., (upper *devonicus — naumovae* Zone), lower Givetian, Blenheim — Gilboa.																
	3?							2?				2?				
	1cf		1cf													
12	61	10	31	4	2		1	2				1				133
Panther Mountain Fm., (upper *devonicus — naumovae* Zone), lower Givetian, *Leclercqia complexa in situ, Blenheim — Gilboa.*																
29	*142*	*1*	*7*	*4?*	*10*		*9*	*8*				*1?*				
				55								*27*				*293*
Williams Island Fm., (devonicus — naumovae Zone), lower Givetian, Hudson Bay Lowlands.																
1cf	1cf			2cf		5cf								1cf		
				1		36							1			48
Cape De Bray, Bird Fiord and Hecla Bay Fms., (*velatus — langii* and *devonicus — naumovae* zones), lower Eifelian — lower Givetian, Canadian Arctic Islands.																
						2?				1?						
2cf	1cf					1cf										
						1						3		2		13
Malbaie Fm., (*velatus — langii* Zone), lower Eifelian, Gaspé.																
							9?									
1cf				3cf			1cf									
							6									20
McAdam Lake Fm., (*velatus — langii* Zone), lower Eifelian, Nova Scotia.																
							2?									
1cf											2					5
Sextant Fm., (*douglastownense — eurypterota* Zone), upper Emsian, Hudson Bay Lowlands.																
										1?	1?	1?	1?			
									2cf				1cf	1cf		
										3	1		4	3		19
Campbellton Fm., (upper *annulatus — sextantii* and lower *douglastownense — eurypterota* zones), upper Emsian, New Brunswick.																
									2?		1?					
									1cf							
									1	4	12	2	1			24
Campbellton Fm., (*douglastownense — eurypterota* Zone), upper Emsian, *Leclercqia* sp. nov. *in situ*, New Brunswick.																
										2?	2?					
									2	80	57					143
Battery Point Fm., (upper *annulatus — sextantii* and lower *douglastownense — eurypterota* zones), upper Emsian, Gaspé.																
												1		3	1	5
Stooping River Fm., (*annulatus — sextantii* Zone), middle Emsian, Hudson Bay Lowlands.																
												3?			2?	
										1	1	1			1	9

* Type IV, and Subtypes VA and VB, were seen in SEMs of *in situ* material from Blenheim-Gilboa. No attempt was made to count SEM material, but these types and subtypes were rare. In the count of the light microscope slides of the Panther Mountain Formation, only a single specimen, possibly assignable to Type IV, was seen.

Fig. 15 *Acinosporites lindlarensis*, light photomicrographs of dispersed spores, Malbaie Formation, *velatus-langii* Zone. All magnifications × 1,000. (a–b) Subtype II?B, distal polar view: (a) low sculptural elements and basal 'tuberculae' only slightly elevated; (b) thin intexine almost equivalent in thickness to the exoexine. (c–e) Subtype cf. IC: (c) distal polar view with biform sculpture crowded except toward the equator; (d) median focus with curvatural spinae and polygonal distal spine bases; (e) part of the spore with curvatural spinae. (f) Subtype IIA, proximal polar view, specimen with subtriangular amb showing prominent Y-folds, small, distal, biform elements and small, slender Type I curvatural spinae. (g–h) Subtype cf. IC, broken, slightly tipped specimen: (g) variable proximal sculpture and stout curvatural spinae; (h) crowded, stout, distal, biform elements.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because the mature *Leclercqia* sp. nov. spores are closely similar to the immature spores of *L. complexa*. Furthermore, the morphographic ranges of types and subtypes overlap within the temporal sequence. The contemporaneous dispersed and *in situ* spores reflect the two plant species and the palynodemes — 'palynodemes' show progressively shifting sculptural modes with geological time. This is shown in Table 1: Emsian palynodemes — 'palynodemes' are dominated first by spores of Type VI ('parvulus' tendency) and later by Type V, whereas Eifelian and Givetian palynodemes — 'palynodemes' consist largely of subtypes of I and II, with subtypes of I increasing in abundance in younger strata. There is thus a need for further data from other localities to test, modify and amplify the succession suggested here.

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Fig. 16 *Leclercqia* sp. nov. *in situ* spores (a–d) and *Acinosporites lindlarensis* dispersed spores (e–f), light photomicrographs; Campbellton Formation, *douglastownense–eurypterota* Zone. All magnifications × 1,000. (a–b) Subtype VD, tipped specimen: (a) proximal view with biform 'tuberculae' and coarse proximal sculpture; (b) distal focus showing acanthomammillate sculpture and narrow canaliculae. (c–d) Subtype VD, proximal polar view: (c) proximal focus showing low lips and curvatural sculptural elements some of which have extended spinose terminations; (d) distal focus showing acanthomammillate to foveolate distal sculpture. (e–f) Subtype cf. V, matrix surrounding *Leclercqia* sp. nov.: (e) tipped specimen with split exoexine, laevigate 'intexine' and crowded, small sculpture; (f) distal polar view showing small sculpture like Type VI but forming a polygonal pattern like IA–B.

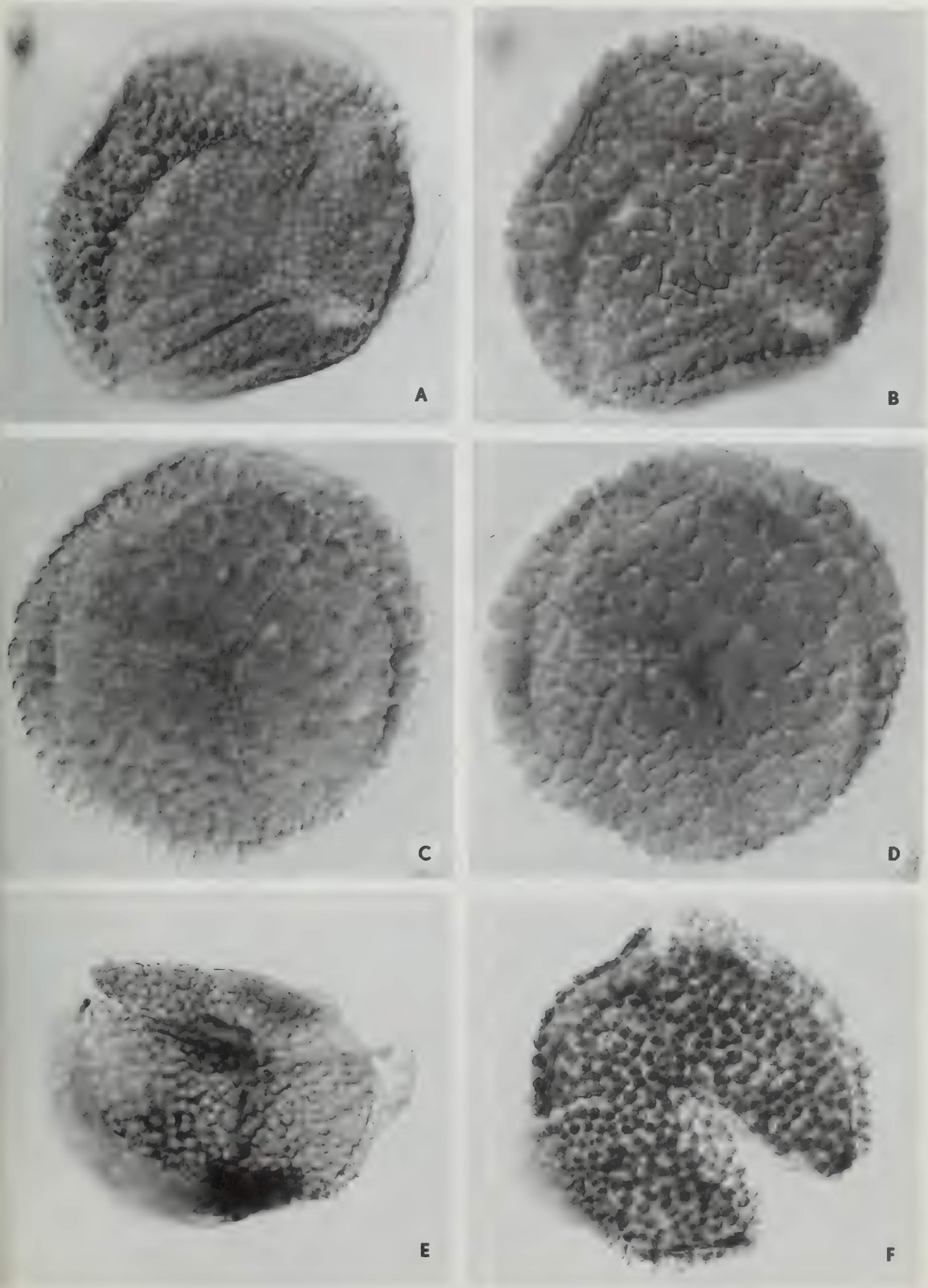
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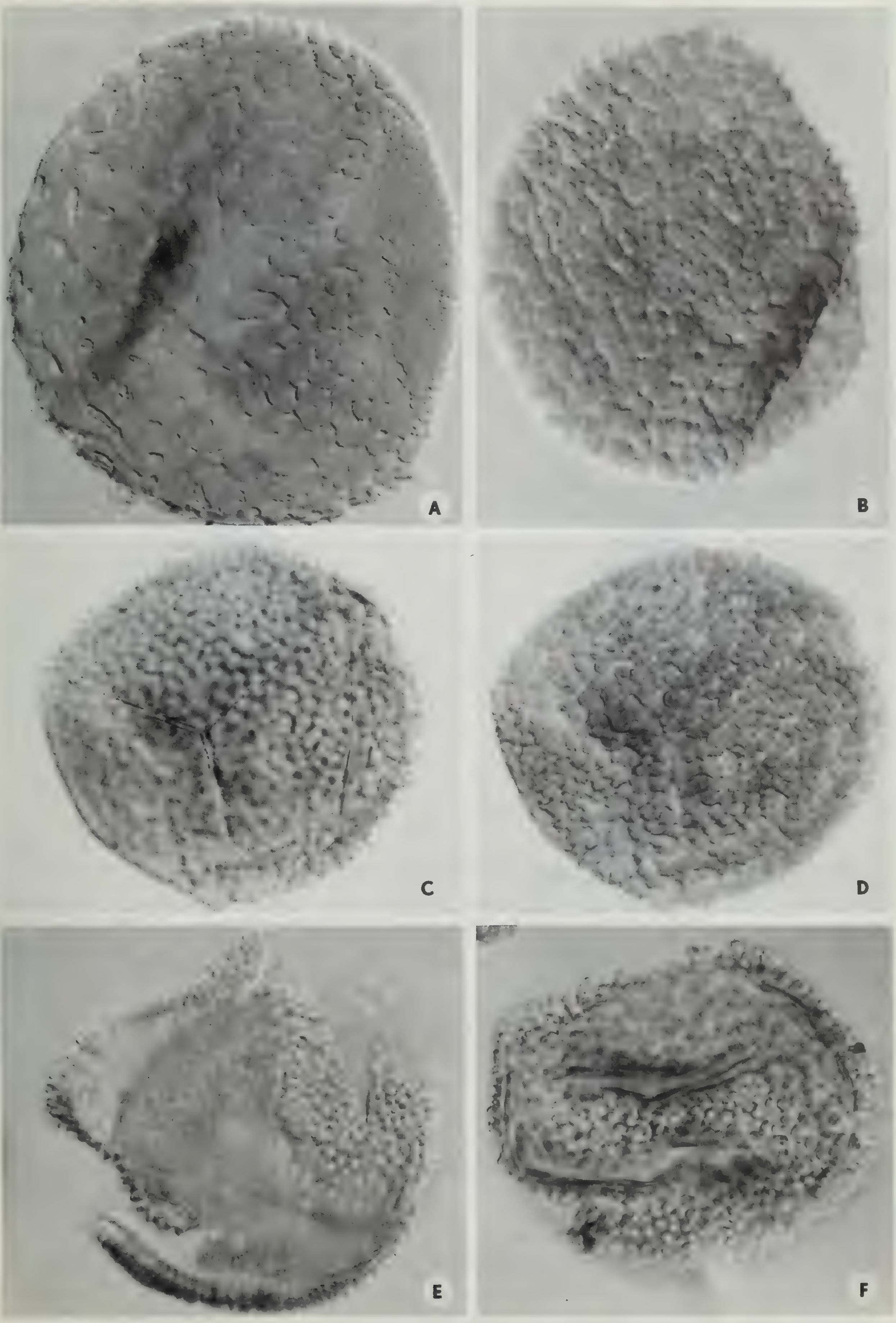
Fig. 17 *Leclercqia* sp. nov. *in situ* spores (a–b) and *Acinosporites lindlarensis* dispersed spores (c–f); (a–d) Campbellton Formation *douglastownense–eurypterota* Zone; (e–f) Stooping River Formation, *annulatus–sextantii* Zone, light photomicrographs. All magnifications × 1,000. (a) Subtype VC, lateral compression showing foveolate distal area with slender coni, merging into typical acanthomammillate sculpture in the subequatorial region, no differentiation of curvatural sculpture and small proximal sculpture. (b) Subtype VC, distal polar view showing small biform elements and broad sinuous ridges. (c–d) Subtype VD–VI, matrix of *Leclercqia* sp. nov. Specimen with smaller sculpture than typical type VD spores: (c) proximal focus showing simple trilete sutures; (d) distal focus showing acanthomammillate sculpture. (e) ?Type VI, broken specimen with crowded, small, biform elements. (f) ?Subtype VD, broken specimen showing irregular curvatural spinae.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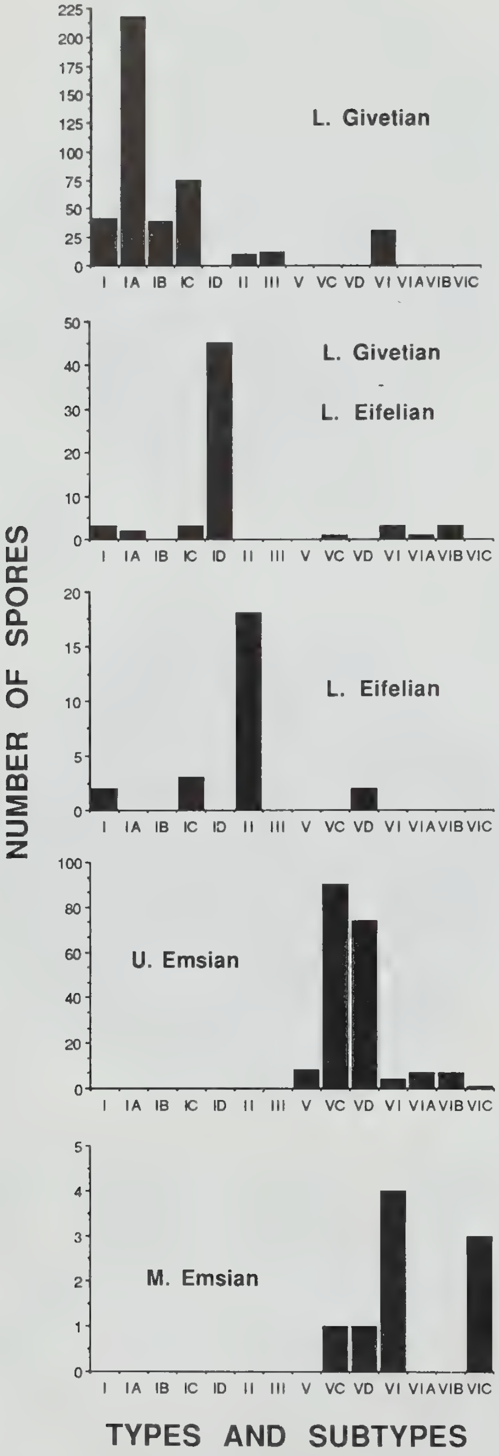

Fig. 18 Types and subtypes grouped into palynodemes — 'palynodemes' for five stratigraphical intervals, based on data in Table 1. Note that different vertical scales are used.

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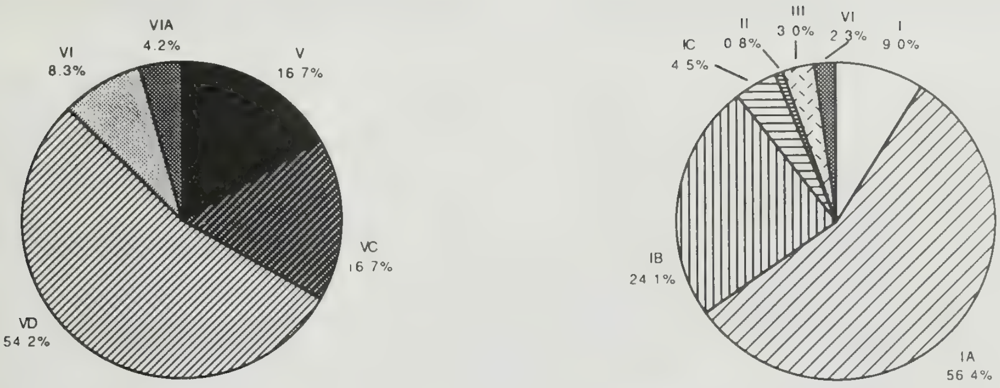
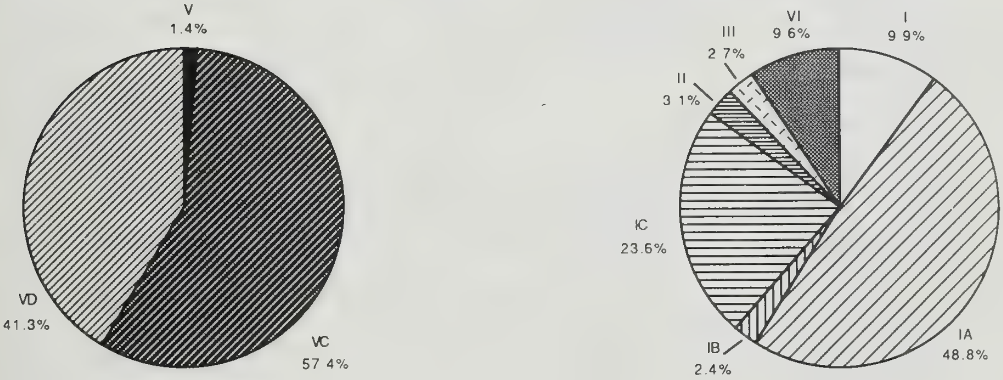


A. Leclercqia sp. nov. matrix,
Dalhousie Junction, upper Emsian

B. Leclercqia complexa matrix,
Blenheim/Gilboa, lower Givetian



C. Leclercqia sp. nov. in situ,
Dalhousie Junction, upper Emsian

D. Leclercqia complexa in situ,
Blenheim/Gilboa, lower Givetian

Fig. 19 Comparison between dispersed and *in situ* assemblages of spore types and subtypes from Dalhousie Junction and Blenheim-Gilboa.

APPENDIX I: REGISTER OF LOCALITIES

Locality no.	Locality	Formation	Location on Fig. 1
None	New York State, Schoharie County, along Schoharie Creek, cliff in west flank of Brown Mountain adjacent to electrical generating plant.	Panther Mountain	1
None	New York State, Schoharie County, Blenheim-Gilboa borehole B1, 1143.8 m N60E of reservoir near power plant.	Panther Mountain	1
GSC A–005368	Eastern Quebec, south shore of Gaspé Bay, 47 m north of small stream about 1.6 km northwest of Cap Rouge.	Battery Point	3
A–007102	Eastern Quebec, south shore of Gaspé Bay, 385 m north of Bois Brulé Brook.	Battery Point	3
A–007115	Eastern Quebec, south shore of Gaspé Bay, 732 m south of second stream south of Bois Brulé Brook.	Battery Point	3
A–007132	Eastern Quebec, south shore of Gaspé Bay, 59.5 m southeast of conglomerate of Pointe Jaune.	Malbaie	3
A–007138	Eastern Quebec, south shore of Gaspé Bay, 482 m southeast of first stream south of Pointe Jaune.	Malbaie	3
A–007850	Northern Ontario, Moose River Basin, Argor ETA No. 2 well, Kiasko River, 50°41′30″N, 80°48′00″W, 41.7 m depth.	Sextant	5
A–008057	Northern Ontario, Moose River Basin, Ontario Department of Mines Jaab Lake No. 1 well, 51°11′54″N, 82°56′00″W, 48.0–48.6 m depth.	Williams Island	6
A–008058	As above, but 51.7–52.3 m depth.	Williams Island	6
A–008100	As above, but 191.2–191.8 m depth.	Stooping River	6
A–008104	As above, but 204.6–205.2 m depth.	Stooping River	6
A–008785	Northern Ontario, Moose River Basin, Argor ETA No. 2 well, Kiasko River, 50°41′30″N, 80°48′00″W, 46.3–46.4 m depth.	Sextant	5
C–007678	Sheills Peninsula, Devon Island, 76°16′30″N, 95°15′00″W, 1.1 km from mouth of unnamed creek at Inglis Bay.	Bird Fiord	9
C–091951	Southwestern Ellesmere Island, western margin of inner Goose Fjord, 76°52′52″N, 88°43′01″W.	Hecla Bay	10
C–091990	Southwestern Ellesmere Island, river ca. 23 km south-southwest of Sor Fjord, 77°04′49″N, 84°34′17″W.	Hecla Bay	12
C–129628	Northeastern Melville Island, 75°52′N, 106°18′W, ca. 12 km east of Weatherall Bay	Cape De Bray	7
O–094437	Northern Nova Scotia, Cape Breton Island, 46°01′30″N, 60°24′40″W, roadcut 0.56 km northwest of McAdam Lake.	McAdam Lake	4
O–095530	Northern New Brunswick, south side of lower Restigouche River, 760 paces west of first access road to beach west of Dalhousie Junction.	Campbellton	2
O–096376	Northern New Brunswick, south side of lower Restigouche River, 48°02′30″N, 66°30′40″W, 0.8 km west of Dalhousie Junction.	Campbellton	2
O–096385	As above but 0.8 km west of Dalhousie Junction, about 0.6 m above high tide.	Campbellton	2
O–098401	Northern New Brunswick, south side of lower Restigouche River, 48°02′30″N, 66°30′40″W, 1200 m west of Dalhousie Junction.	Campbellton	2
O–098402	As above, but 1245 m west of Dalhousie Junction.	Campbellton	2
O–098403	As above, but 1072 m west of Dalhousie Junction.	Campbellton	2
O–098404	As above, but 925 m west of Dalhousie Junction.	Campbellton	2
O–100837	Bathurst Island, south of Dundee Bight, 75°50′00″N, 100°10′00″W, 226.0 m above base of section.	Bird Fiord	8
O–100909	Southwestern Ellesmere Island, north of Bird Fjord, 77°12′30″N, 87°02′00″W.	Bird Fjord	11

GSC = Geological Survey of Canada; Last column refers to numbers on Fig. 1.

APPENDIX II: Publications containing reference to *Acinosporites lindlarensis*

Author(s)	Date	Illustrations	Designation in Publication	Geographic Location	Designated age	Comment
Arkhangel'skaya	1976		*Geminospora treverica*	European USSR	Early Eifelian	
Arkhangel'skaya	1985a		*G. treverica*	European USSR	Late Emsian	
Arkhangel'skaya	1985b	Pl. 5, fig. 9,10	*G. treverica*	European USSR	Late Emsian to early Givetian	
Bär & Riegel	1974		*G. treverica*	Ghana	Givetian	
Brice et al.	1979		*Aneurospora* cf. *heterotunda* (sic)	France	Early Givetian	Assumed to be var. *lindlarensis*
Burjack et al.	1987	Pl. 1, Fig. 2	(var.) *lindlarensis*	Brazil	Late Eifelian to late Givetian	
Cramer	1969	Pl. 2 fig. 27	'Indeterminate'	Spain	Late Eifelian to Givetian	Probably var. *lindlarensis*
Edalat	1974		*lindlarensis*	Rhineland	Late Emsian	
Grey	1991	Pl. 1, fig. 9	*Dibolisporites* sp. cf. *echinaceus*	W. Australia	Late Givetian	Probably var. *lindlarensis*
			lindlarensis	W. Australia	Late Givetian	
Grey	1992	Pl. 1, figs. 6–8	*lindlarensis* ?	W. Australia	Late Givetian	Illustrated specimens not *lindlarensis* ?
		Pl. 14, figs. 1–4	*Dibolisporites* sp. cf. *D. echinaceus*	W. Australia	Late Givetian	Probably var. *lindlarensis*
Le Hérissé	1983	Pl. 4, figs. 9a–b, 10; Text–fig. 16	var. *minor*	France	Late Siegenian	
Lesuisse et al.	1979	Pl. 5, fig. 15	var. *minor*	Belgium	Late Emsian	
Lipatova	1984	Pl. 2, fig. 13	*G. treverica*	Siberia	Recycled	? Misidentified
Loboziak & Streel	1989	Pl. 2, figs. 5,6	(var.) *lindlarensis*	Tunisia, Libya	Late Emsian to early Frasnian	
Loboziak, Streel & Weddige	1990		*lindlarensis*	Germany	Early Givetian	
Marshall & Allen	1982	Pl. 30, figs. 2,5	var. *minor*	Shetland	Givetian	
Massa & Moreau-Benoit	1976	Pl. 3, fig. 3	*G. treverica*	Libya	Late Emsian and early Eifelian	
McGregor	1973	Pl. 6, figs. 17–21	(var.) *lindlarensis*	Gaspé (Canada)	Late Emsian and Eifelian	Also McGregor 1977
McGregor	1979a	Pl. 1, fig. 19	var. *lindlarensis*	Ontario (Canada) + unspecified	Late Emsian to early Givetian	
McGregor	1979b		(var.) *lindlarensis*	Unspecified	Late Emsian to early Givetian	
McGregor	1984	Pl. 2, fig. 21	var. *lindlarensis*	Bolivia	Late Emsian and early Eifelian	Identification questioned
McGregor & Camfield	1976	Pl. 5, figs. 2,3	var. *lindlarensis*	Ontario (Canada)	Late Emsian to Givetian	
		Pl. 5, figs. 4,5	var. *minor*	Ontario (Canada)	Late Emsian to Givetian	
McGregor & Camfield	1982	Pl. 1, figs. 9,10; Text-fig. 10	var. *lindlarensis*	Canadian Arctic Is.	Early Eifelian to early Givetian	
McGregor & Playford	1992	Pl. 1, fig.1	var. *lindlarensis*	Eastern Canada	Late Emsian to late Givetian	
		Pl. 1, fig. 2	var. *lindlarensis*	Australia	Givetian	
		Pl. 1, fig. 9	var. *minor*	Ontario (Canada)	Late Emsian to late Givetian	
		Pl. 1, fig. 10	var. *minor*	W Australia	Early Frasnian	
McGregor & Uyeno	1972		(var.) *lindlarensis*	Canadian Arctic Is.	Eifelian and early Givetian	

Moreau-Benoit	1980		*G. treverica*	Libya	Late Emsian and Eifelian	
		Pl. 13, fig. 6	*G. libyensis*	Libya	Early and late Givetian	? var. *lindlarensis*
Moreau-Benoit	1989	Pl. 1, fig. 7	var. *lindlarensis*	Libya	Late Eifelian	Illustrated specimen misidentified ?
Moreau-Benoit & Massa	1988		*G. treverica*	Libya	Late Emsian	
Perez-Leyton	1990		*lindlarensis*	Bolivia	Late Eifelian, late Givetian and early Frasnian	
Ravn & Benson	1988	Pl. 5, figs. 1–3	var. *lindlarensis*	Georgia (USA)	Late Emsian and Eifelian	
Richardson	1974		*lindlarensis*	Canada, Belgium, Germany	Late Emsian to early Givetian	
Richardson & McGregor	1986	Pl. 6, fig. 8	var. *lindlarensis*	various	Late Emsian to early Givetian	
Riegel	1968	Pl. 19, figs. 11–16	(var.) *lindlarensis*	Rhineland	Mid Eifelian	Incl. holotype
Riegel	1973	Pl. 16, figs. 5–7	*G. treverica*	Rhineland	Late Emsian and early Eifelian	Incl. holotype
Riegel	1974		(var.) *lindlarensis*	Rhineland	Early to mid Eifelian	
			Acinosporites treverica	Rhineland	Early Eifelian	
Riegel	1982		(var.) *lindlarensis*	Rhineland	Late Emsian to early Givetian	
Schweitzer	1983	Pl. 2, fig. 7	(var.) *lindlarensis*	Rhineland	Early Eifelian	holotype
Steemans	1989	Pl. 18, figs. 7–9, Text-fig. 35	*lindlarensis*	Belgium, Germany, Romania	Late Gedinnian to late Siegenian	Varieties not distinguishable
Steemans & Gerrienne	1984		*lindlarensis*	Belgium	Late Gedinnian	Varieties not distinguishable
Streel	1972	Pl. 2, figs. 1–7	*Aneurospora* cf. *heterodonta*	New York State (USA)	Late Givetian	'Associated with *Leclercqia complexa*'
Turnau	1985		*lindlarensis*	Poland	Late Emsian or early Eifelian	
Turnau	1986	Pl. 7, figs. 9, 12, 13	(var.) *lindlarensis*	Poland	Late Emsian or early Eifelian	
Vaitekunene	1983		*lindlarensis*	Lithuania	Late Eifelian	
Van der Zwan	1980	Pl. 1 fig. 9; Pl. 2, figs. 1,2	var. *minor*	Ireland	Late Emsian	

APPENDIX III: DISPERSED SPORES: REGISTER OF ILLUSTRATED SPECIMENS

Figure	Slide		Negative	England finder ref. (Zeiss Photomic.)	GSC Type specimen No.
12a	SUNY Binghamton-	2002–M–32	PY 1397	S41/4/T42/1	103908
12b		‘	PY 1399	‘	‘
12c		‘	PY 1397	‘	‘
12d		2002–M–13	PY 1431	H53	103909
12e		‘	PY 1430	‘	‘
12f		‘	‘	‘	‘
12g		2002–M–32	PY 1401	M63/4/M63/1	103910
12h		‘	PY 1400	‘	‘
12i		2002–M–14	PY 1436	L54/3	103911
12j		‘	PY 1438	‘	‘
12k		2002–M–22	PY 1415	P47/4	103912
12l		‘	PY 1416	‘	‘
12m		2002–M–21	PY 1428	G49/4	103913
12n		2002–M–32	PY 1396	L38/2	103914
13a		329/24/T/21*	PY 1792	(175´1146)*	103915
13b		‘	PY 1798	(244 1146)*	103916
13c		‘	PY 1796	(233 1172)*	103917
14a	GSC	A–008058/22	PY 1556	W27/4	96756
14b		‘	PY 1557	‘	‘
14c		A–008057/22	PY 1658	M51/3/N51/1	96757
14d		‘	PY 1654	‘	96758
14e		‘	PY 1655	‘	‘
14f		O–95530	PY 1772	U64/1	103918
14g		A–008057/22	PY 1662	E48/4	96760
14h		‘	PY 1664	‘	‘
14i		‘	PY 1663	‘	‘
14j		A–008058/21	PY 1554	X43/4/X44/3	96761
15a	GSC	A–007132/21	PY 1742	066/4	96762
15b		‘	PY 1743	‘	‘
15c		A–007132/22	PY 1749	M/39/4	96763
15d		‘	PY 1748	‘	‘
15e		‘	PY 1747	‘	‘
15f		A–007132/21	PY 1739	M48	96764
15g		A–007132/22	PY 1744	L40/3	96765
15h		‘	PY 1746	‘	‘
16a	GSC	O–096385/x	PY 1676	Q38/R38	103919
16b		‘	PY 1678	‘	‘
16c		‘	PY 1691	X40/4	103920
16d		‘	PY 1692	‘	‘
16e		O–96376/21	PY 1766	V58/4	96766
16f		‘	PY 1769	D29/4/D30/3	98377
17a	GSC	O–096385/H–1	PY 1730	S62	103921
17b		‘	PY 1733	Y63/3	103922
17c		O–96376/21	PY 1762	T30/2/S31/3	96767
17d		‘	PY 1764	‘	‘
17e		A–008104/11	PY 1783	R44/4	96768
17f		A–008104/9	PY 1779	K46/4	96769

Negatives are held at The Natural History Museum, London. All specimens are housed in the National Palynological Type Collection of the Geological Survey of Canada in Ottawa. (* Oversized slide; coordinates refer to Zeiss photomicroscope II, number 65800, not England finder Ref.)

12c K

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